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Taxonomy of the arthrodire *Phlyctaenius* from the Lower or Middle Devonian of Campbellton, New Brunswick, Canada

V. T. Young

Geology series Vol 37 No. 1 30 June 1983

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Taxonomy of the arthrodire *Phlyctaenius* from the Lower or Middle Devonian of Campbellton, New Brunswick, Canada

V. T. Young

Department of Palaeontology, British Museum (Natural History), Cromwell Road, London SW7 5BD

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Synopsis

The species of the Lower/Middle Devonian arthrodire *Phlyctaenius* are reviewed in the light of new material. The new species *P. stenosus* is described and diagnoses of previous species are emended. A multivariate analysis is used to support species recognition. It is suggested that some features hitherto used to distinguish species are invalid, since they are shown to be highly variable. It is also suggested that previous restorations of *Phlyctaenius* are composites of more than one species: a new restoration is given here.

Introduction

In 1971 the British Museum (Natural History) received a collection of fossil fishes collected by Dr W. Graham-Smith and Professor T. S. Westoll from the Devonian of Campbellton, New Brunswick, Canada. Amongst the collection there were many specimens of the arthrodire placoderm *Phlyctaenius*, including twelve skull roofs and many isolated but well-preserved thoracic plates.

It became evident that three species of Campbellton *Phlyctaenius* could be recognized: the type species *P. acadicus* (Whiteaves), *P. atholi* (Pageau) and a new species described below. It also became apparent that the most comprehensive description (Heintz 1933) of *P. acadicus* is based on information from more than one species. Further anatomical information is also provided by these additional specimens. Since *P. acadicus* is often cited in discussions of arthrodire phylogeny it is desirable to revise the taxonomy and to attempt a new restoration of the Campbellton species. These are the primary objectives of this paper.

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Specimens of *Phlyctaenius* from Campbellton were first described by Whiteaves (1881, 1888) as *Coccosteus acadicus*. Further material was described by Traquair (1890*a*, *b*, *c*, 1893) who proposed the name *Phlyctaenius*; Woodward (1891, 1892*a*, *b*) commented on these early descriptions. Heintz (1933) provided a detailed description, used by subsequent authors (Denison 1958, 1978; Goujet 1975; Miles & Dennis 1979; Dennis & Miles 1979*a*, *b*, 1980; Young 1979, 1980, 1981; Young & Gorter 1981) as the basis for comparisons with presumed relatives (*Dicksonosteus*, groenlandaspids). Since Heintz' description many species from the Devonian of Europe have been assigned to *Phlyctaenius*, but these are now placed in other genera (Denison 1978:60).

Materials and methods

The material used in this study is in the British Museum (Natural History), London, the Royal Scottish Museum, Edinburgh, and the National Museum of Canada, Ottawa. Specimens in the two latter institutions are referred to by register number, prefixed by RSM or NMC respectively. Specimens in the British Museum (Natural History) are referred to simply by register number. All of the material is from Campbellton, New Brunswick, Canada. The early collections are not precisely localized, but the material collected by Graham-Smith and Westoll comes from half a mile west of Campbellton. The similarity of the matrix between this material and that previously collected suggests that all of it is from the same locality.

The fish material comes from the Gaspé Sandstone Series (described by Logan 1846, 1863), the age of which is uncertain (Alcock 1935, McGerrigle 1950, Pageau 1968), being considered by some authors Lower Devonian and others Middle Devonian. Alcock (1935) proposed that the base of the Gaspé Sandstone marks the beginning of the Middle Devonian; McGerrigle (1950) divided the middle part of the Gaspé Sandstone into the older York River and younger Battery Point Formations, which together he believed were of Middle Devonian age. According to Pageau (1968) the fish fauna occurs in the Battery Point Formation, which he suggests belongs to the lower part of the Middle Devonian, with the Gaspé Sandstone Series crossing the Lower/Middle Devonian boundary. The Gaspé Sandstone Series contains abundant, well-preserved spores (McGregor 1973, 1977) which indicate that the Lower/Middle Devonian boundary lies in the upper part of the Battery Point Formation (McGregor 1973: fig. 4). The fish fauna is therefore considered to be of latest Lower or earliest Middle Devonian age.

In the following study the specimens were sorted into three groups and original observations were tested by a multivariate analysis. As with many primitive arthrodires the skull roofs tend to remain intact and, in this instance, provide the bulk of the evidence for species recognition. The abbreviations of the separate plates are mainly those of Miles (1971); see list below.

Explanation of abbreviations used in text and figures:

ADL	anterior dorsolateral	PM	postmarginal
AL	anterior lateral	PMV	posterior median ventral
AMV	anterior median ventral	PN	postnasal
AV	anteroventral	PNu	paranuchal
AVL	anterior ventrolateral	PrO	preorbital
C	central	PtO	postorbital
IL	interolateral	PVL	posterior ventrolateral
M	marginal	R	rostral
MD	median dorsal	RP	rostralo-pineal
Nu	nuchal	SM	submarginal
P	pineal	SO	suborbital
PDL	posterior dorsolateral	Sp	spinal
PL	posterior lateral		

The specimens were prepared using a mechanical drilling tool. Where impressions only remain, positive casts were made using silicone or latex rubber. Casts of ornament tubercles were studied with the aid of a scanning electron microscope. Because of the difficulty of examining large bone fragments in the SEM, 'Araldite' casts were made from latex rubber moulds. The casts were coated with 360 Å (36 nm) of gold palladium. Drawings were made with the aid of a Grant Projector and with the drawing tube attached to the Wild stereo microscope.

Taxonomy

Identification of the species

The specimens of skull roofs studied here belong to more than one morphological group. They were divided visually into three groups, based on proportions and characters, corresponding to *Phlyctaenius acadicus*, *P. atholi* and the new species *P. stenosus*.

A multivariate analysis was carried out, using qualitative characters and measurements (numbered 1–10, Fig. 1) of the skull roofs. The characters used in the analysis were those visible in the majority of specimens. They were coded for their alternative states and are discussed in the text below. These characters include the nature of the sutures; the nature of the occipital cross commissural groove and position of the growth centre and the shape of the posterolateral margin of the PNu; the skull roof length relative to the width; the presence or absence of the median postpineal and the nature and arrangement of the ornament tubercles. Ten measurements (Fig. 1) were used; the raw data are deposited on file in the Palaeontology Library, British Museum (Natural History).

The percentage similarity between each pair of specimens was calculated using Gower's (1971) coefficient of similarity. The results were used in a principal co-ordinates analysis to produce a two-dimensional plot in which the distances between the points (representing specimens) most closely correspond to the calculated similarities between the specimens.

The first plot (Fig. 2) used qualitative characters and measurements for 41 specimens out of a total of 43 (two very fragmentary specimens were excluded). From the plot it seems that the specimens may be divided into three groups. One incomplete specimen (P6573d, Fig. 2), at first assigned to *P. acadicus*, appears to have a higher similarity to *P. atholi*: it is uncertain to which group it belongs. A second specimen (P6573e, Fig. 2), probably belonging to *P. stenosus* sp. nov., appears to have a higher similarity to *P. acadicus* or *P. atholi*, but it is incomplete and the lack of data may account for its unexpected position on the plot.

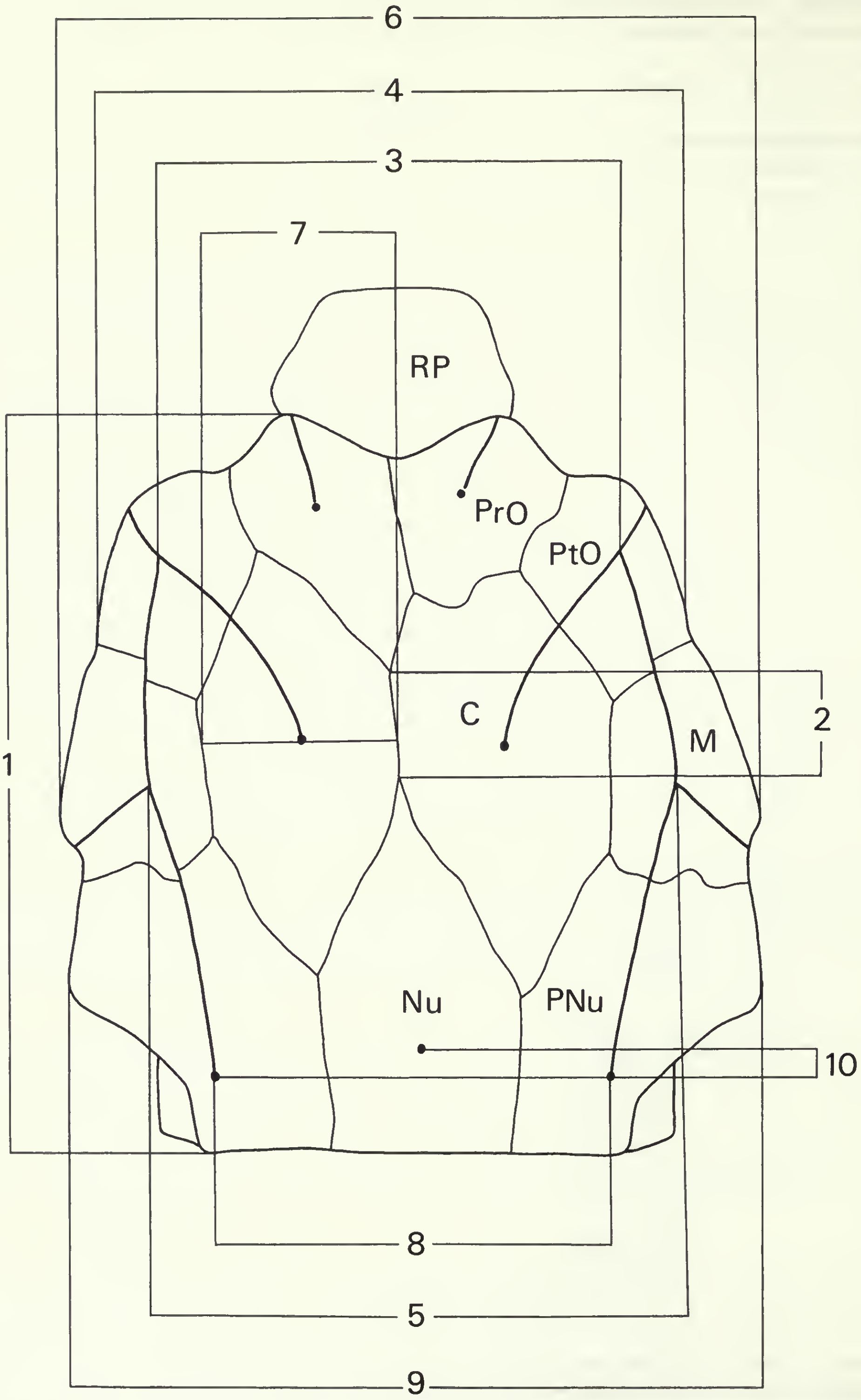
Some of the specimens included on this first plot have many missing values and it was felt that this may have introduced distortion. So a second plot was prepared for the 34 most complete specimens; that is, excluding those specimens with more than 10 missing values. The resulting plot is almost identical to the first.

A third plot (Fig. 3) was constructed from measurements only, to test whether the grouping was entirely due to the qualitative characters and whether or not it was biased. Specimens with more than four missing values were excluded. Although this left only 22 specimens, the result is a grouping pattern similar to that of the first two plots, and corresponding to the groupings originally recognized.

Thus from the plot it seems that *P. acadicus*, *P. atholi* and *P. stenosus* are distinct groups. The specimens grouped as *P. atholi* include two described by Pageau (1969), both with a median postpineal, and eight others showing the anterior area all without this plate. This suggests that the presence of a median postpineal is a variation and not a specific character (see pp. 12–13).

For each dimension measured (Fig. 1), a separate sheet of tracing paper was laid over Fig. 3 (the plot incorporating measurements only), and using this as a basis the measured value for each specimen, represented by a point on the figure, was plotted on the sheet at the relevant point.

By doing this, certain trends in the value of each dimension were indicated. The first axis of Fig. 3 shows, from left to right, increase in the value of each dimension corresponding with the size of the specimen: the second axis indicates differences in shape between the specimens and separates the groups. Relatively, specimens of *P. stenosus* tend to have medium to high values for measurements 1–4, and low to medium values for measurements 5–10. Specimens of *P. acadicus* tend to have medium to high values for measurements 1–3 and high values for measurements 4–10. Specimens of *P. atholi* tend to have low to medium values for measure-


6
4
3
7
RP
PrO
PtO
C
M
2
1
Nu
PNu
10
8
5
9

ments 1–4 and medium to high values for measurements 5–10. These character tendencies, interpreted as a result of overlaying measurements on the plot, as described above, can be summarized as follows:

1. Skull roofs of *P. acadicus* tend to be larger overall than those of the other two species;
2. Skull roofs of *P. acadicus* and *P. stenosus* tend to be relatively longer than those of *P. atholi*;
3. Skull roofs of *P. atholi* tend to be relatively narrower anteriorly compared with those of the other two species;
4. Skull roofs of *P. atholi* and *P. acadicus* tend to be relatively wider posteriorly than those of *P. stenosus*; and
5. The growth centre of the PNu occurs in the same transverse plane as that of the Nu in *P. stenosus* but further posteriorly in the other two species.

Diagnoses

Order **ARTHRODIRA** Woodward, 1891
Suborder **PHLYCTAENIOIDEI** Miles, 1973
Infraorder **PHLYCTAENII** Miles, 1973
Family **PHLYCTAENIIDAE** Fowler, 1947
Genus ***PHLYCTAENIUS*** Traquair, 1890*a*
[= *Phlyctaenaspis* Traquair, 1890*c*]

Diagnosis. See Denison (1978: 59).

Type species. *Phlyctaenius acadicus* (Whiteaves 1881).

Remarks. The name *Phlyctaenius* was originated by Traquair (1890*a*: 20), but he later (1890*c*: 144) changed it to *Phlyctaenaspis* since he believed the name *Phlyctaenius* to be preoccupied by *Phlyctaenium* Zittel, a fossil sponge. However, *Phlyctaenius* is the valid name for this genus (White 1969: 302 footnote; Fowler 1947: 6).

Two points in Denison's 1978 diagnosis could not be confirmed in material examined here: the PMs were stated to be large, and the endocranium perichondrally ossified (see p. 17). The source of the reference to the size of the PMs seems to be Denison (1958: 511, fig. 105, specimen number P5972), where he records an impression of a plate suspected to be large, although he does not say that the PM is from an impression.

Phlyctaenius acadicus (Whiteaves 1881)

Figs 4; 5A, D; 9A; 10; 11A; 12A; 16D; 18A, D, F

1881	*Coccosteus acadicus* Whiteaves: 94; text-fig. 1.
1888	*Coccosteus acadicus* Whiteaves; Whiteaves: 93; pl. 9, figs 1, 3 (not figs 2, 4); text-fig. 2.
1890*a*	*Phlyctaenius acadicus* (Whiteaves) Traquair: 20.
1890*b*	*Phlyctaenius acadicus* (Whiteaves); Traquair: 60.
1890*c*	*Phlyctaenaspis acadica* (Whiteaves) Traquair: 144.
1891	*Phlyctaenaspis acadica* (Whiteaves); Woodward: 295 (in part).
1892*a*	*Phlyctaenaspis acadica* (Whiteaves); Woodward: 5; pl. 1, fig. 8 (not fig. 7).
1892*b*	*Phlyctaenaspis acadica* (Whiteaves); Woodward: 481, text-fig. 1.

Fig. 1 Outline drawing of skull roof to show measurement parameters used in multivariate analysis: 1. PrO–PNu length of skull roof; 2. Length of mutual C suture; 3. Distance between growth centres of PtOs; 4. Width of skull roof at level of PtOs; 5. Distance between growth centres of Ms; 6. Width of skull roof at level of Ms; 7. Width of C (where possible measured on left C); 8. Distance between growth centres of PNus; 9. Width of skull roof at level of PNus; 10. Longitudinal distance between the growth centres of Nu and PNu. The breadth/length index (100B/L) used in the species diagnoses was obtained by expressing measurement 6 as a percentage of measurement 1. The abbreviations for plate names follow those used by Miles (1971); see p. 2.

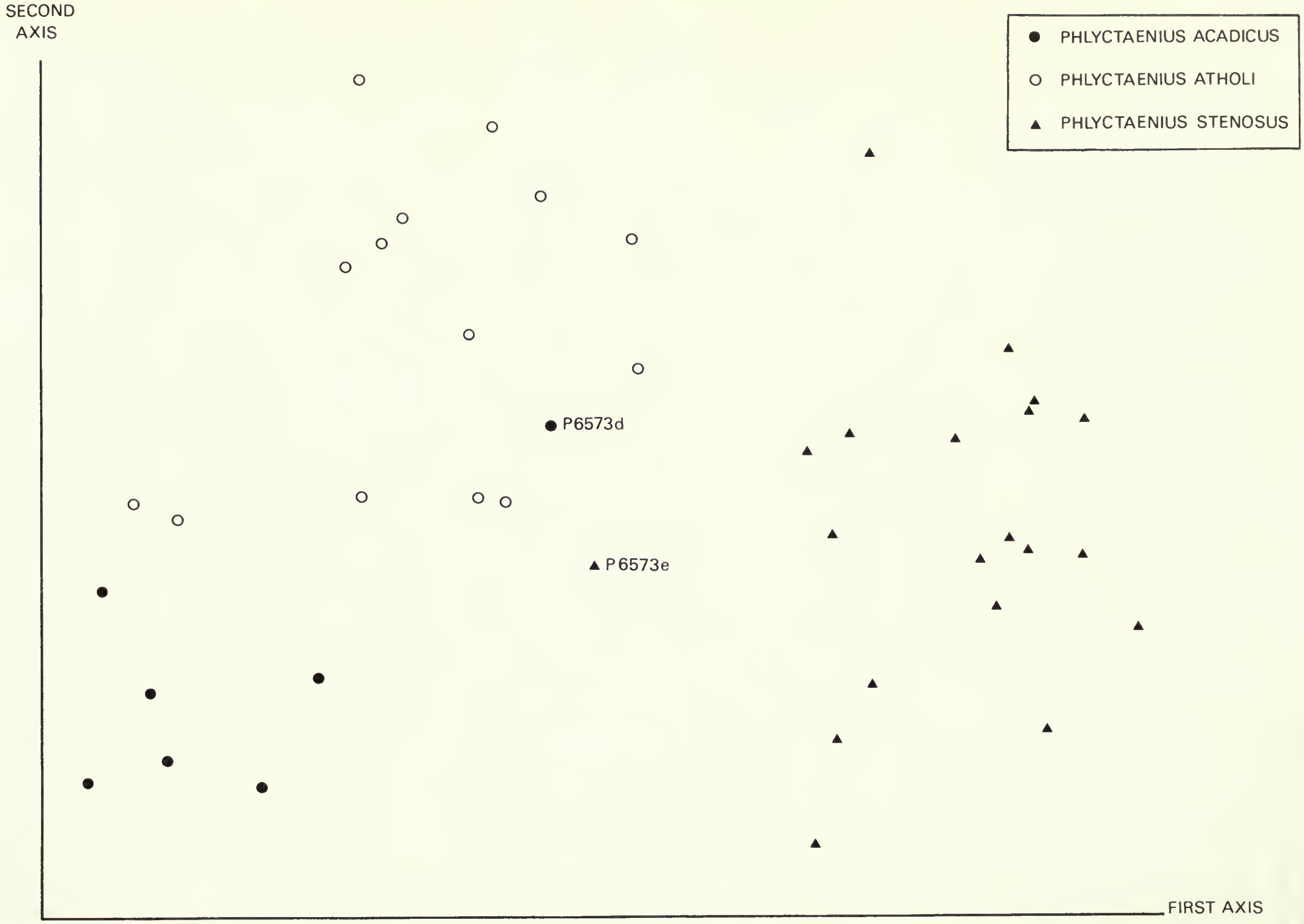


Fig. 2 A plot of the first two principal co-ordinates axes using qualitative characters and measurements.

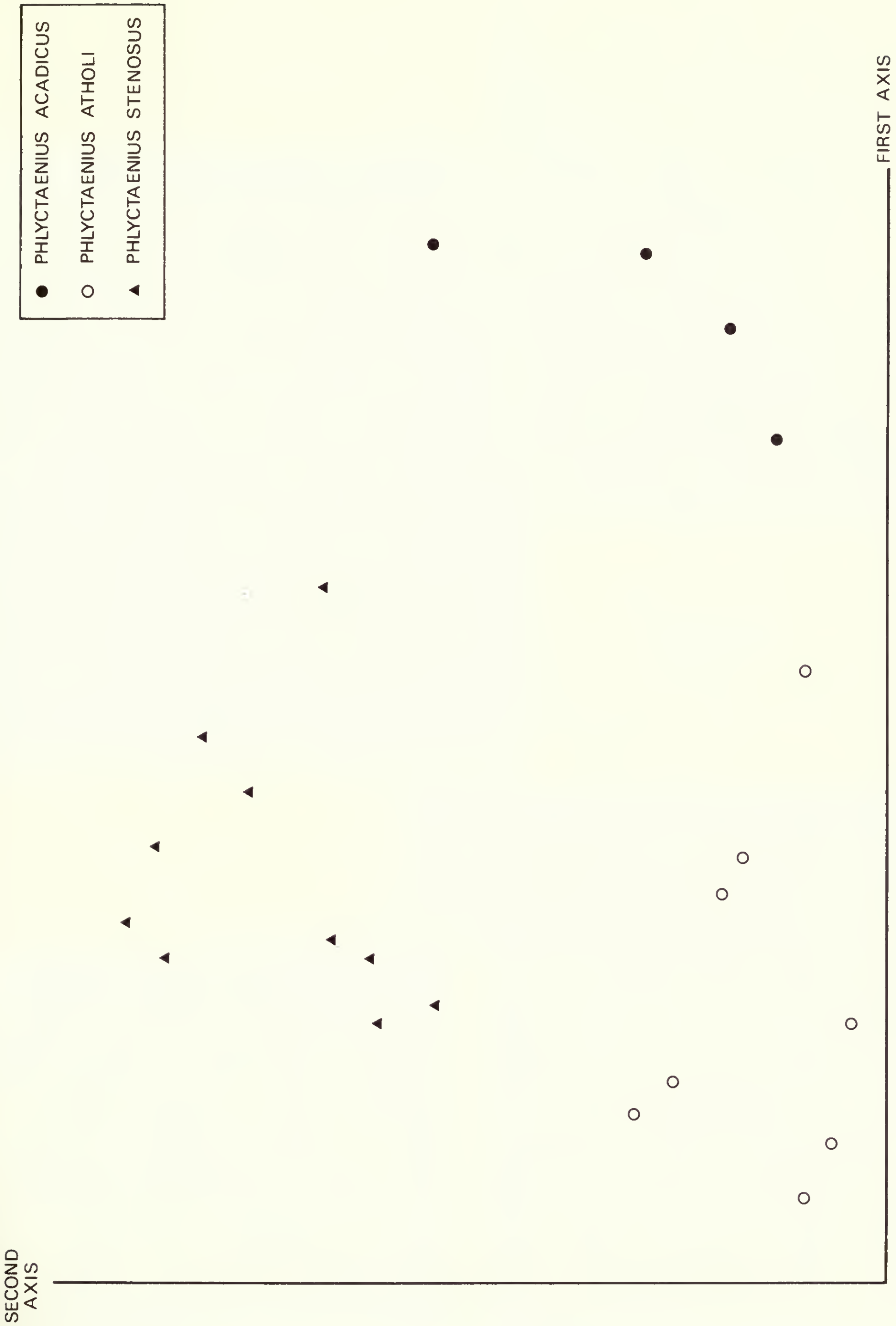


Fig. 3 A plot of the first two principal co-ordinates axes using measurements only.

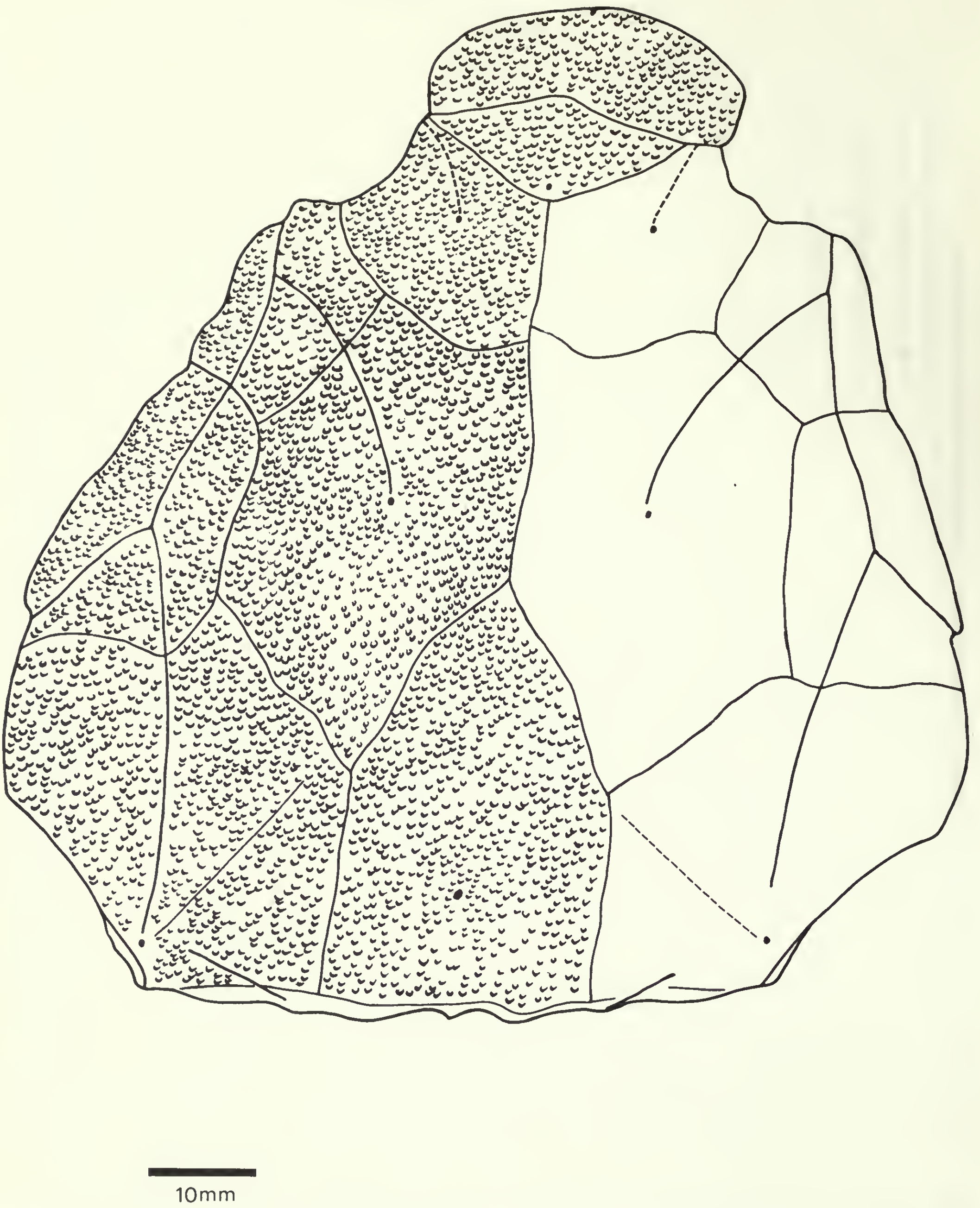
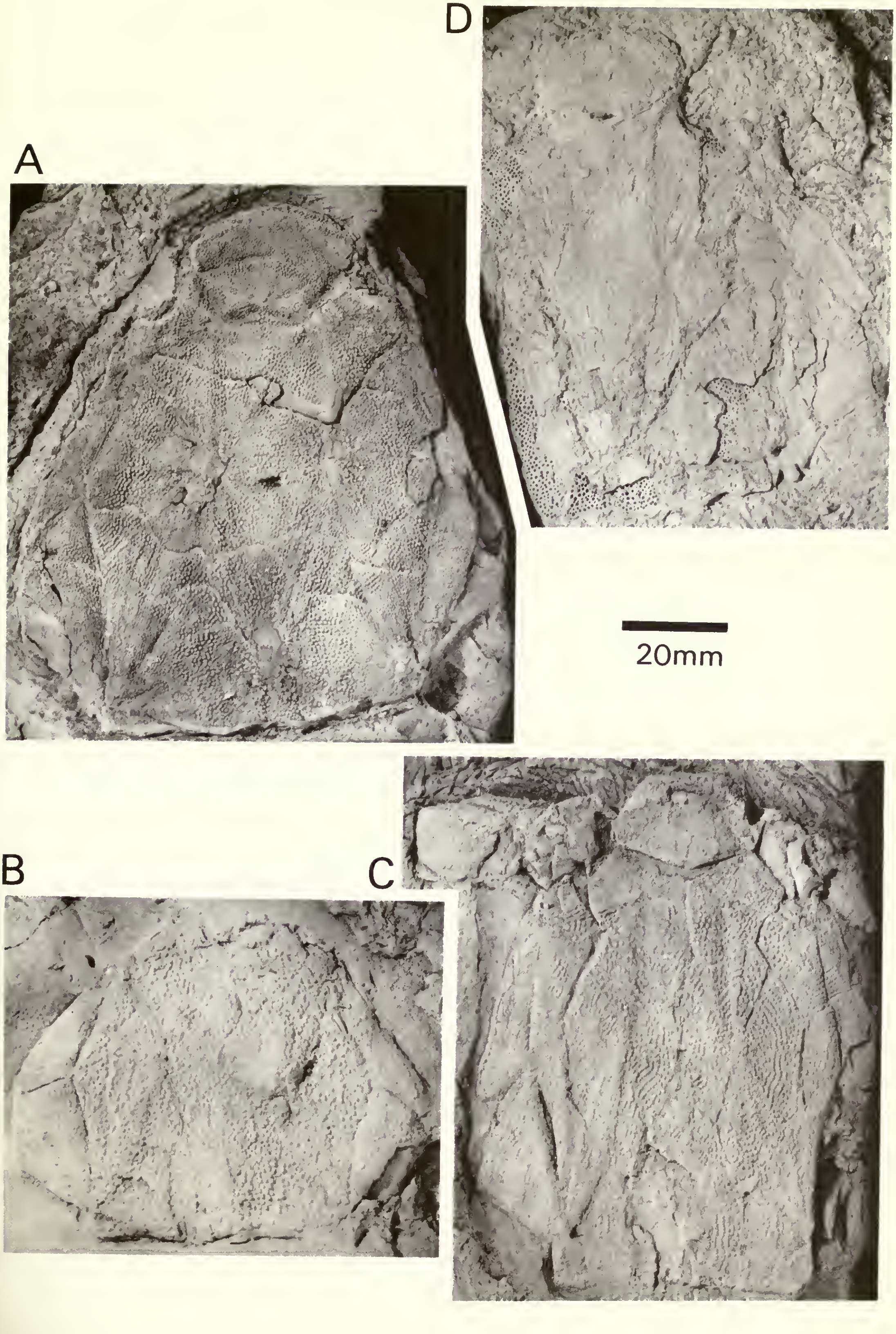


Fig. 4 *Phlyctaenius acadicus* (Whiteaves). Restoration of skull roof based on RSM GY 1897.51.129.

Fig. 5 A. *Phlyctaenius acadicus* (Whiteaves), skull roof, RSM GY 1897.51.129. B. *Phlyctaenius atholi* (Pageau), skull roof, **lectotype** RSM GY 1897.51.123. C. *Phlyctaenius stenosus* sp. nov., skull roof, **holotype** P6555. D. *Phlyctaenius acadicus* (Whiteaves), skull roof, visceral surface, P6554.


D
A
20mm
B
C

1893 *Phlyctaenaspis acadica* (Whiteaves); Traquair: 147, text-fig. 1.
1894 *Phlyctaenaspis acadica* (Whiteaves); Traquair: 370.
1907 *Phlyctaenaspis acadica* (Whiteaves); Whiteaves: 265; pl. 4, figs 3, 4 (not figs 1, 2).
1916 *Phlyctaenaspis acadica* (Whiteaves); Chapman: 212.
1925 *Phlyctaenaspis acadica* (Whiteaves); Stensiö: 165; text-fig. 20 (not fig. 21).
1932 *Phlyctaenaspis acadica* (Whiteaves); Woodward *in* Zittel: 42.
1933 *Phlyctaenaspis acadica* (Whiteaves); Heintz: 127; (not pl. 1), pl. 2, figs 1–8; pl. 3, figs 4–6 (not figs 1–3); text-figs 3 (in part), 5 (in part), 6 (in part) (not text-figs 1, 2, 4).
1938 *Phlyctaenaspis acadica* (Whiteaves); Hussakof: 280.
1951 *Phlyctaenaspis acadica* (Whiteaves); Ørvig: 408; pl. 7, fig. 1.
1957 *Phlyctaenaspis acadica* (Whiteaves); Ørvig: text-fig. 9A.
1957 *Phlyctaenaspis acadica* (Whiteaves); Gross: 20; pl. 6, figs 5–7, 9.
1958 *Phlyctaenaspis acadica* (Whiteaves); Denison: text-figs 107B, 110B, 112K, 113B.
1959 *Phlyctaenaspis acadica* (Whiteaves); Stensiö: 13.
1962 *Phlyctaenaspis acadica* (Whiteaves); Miles: 65.
1963 *Phlyctaenaspis acadica* (Whiteaves); Westoll & Miles: 146; text-fig. 6a.
1964 *Phlyctaenaspis acadica* (Whiteaves); Lehman: 194; pl. 1, fig. E.
1966 *Phlyctaenaspis acadica* (Whiteaves); Gardiner: 32.
1968 *Phlyctaenaspis acadica* (Whiteaves); Miles & Westoll: 399.
1969 *Phlyctaenaspis acadica* (Whiteaves); Miles: 132; text-figs 9f–g (not 9h).
1969 *Phlyctaenaspis acadica* (Whiteaves); Pageau: 810; pl. 25, fig. 1; pl. 29, fig. 5; pl. 30, figs 1, 2, 4–7, 10; text-figs 19.5, 20.7, 21M.
1975 *Phlyctaenius acadicus* (Whiteaves); Goujet: text-fig. 1B.
1978 *Phlyctaenius acadicus* (Whiteaves); Denison: 59; text-fig. 42.
1979*a* *Phlyctaenius acadicus* (Whiteaves); Dennis & Miles: text-fig. 1.

DIAGNOSIS (emended). A species of *Phlyctaenius* in which the skull roof breadth at the level of the M is greater than the PrO–PNu length; 100 B/L index = 110 (excluding RP); posterolateral margin of the PNu straight or gently curved; anterior and lateral margins of the R convex; sutures not evident; ornament tubercles uniformly arranged; tubercles small with pointed, angular peaks; growth centre of PNu at posterolateral margin of the plate, and close to the posterior margin; occipital cross-commissural groove on PNu clearly indicated; postoccipital para-articular process on PNu small; infraorbital canals converge anteriorly; AL more than twice as tall as wide.

HOLOTYPE. NMC 2774, a cranial shield. Restigouche River, Campbellton, New Brunswick, Canada.

HORIZON AND LOCALITY. Latest Lower or earliest Middle Devonian, Campbellton, New Brunswick, Canada.

MATERIAL. Specimens showing skull roofs: a cast of the holotype; RSM GY 1897.51.129, an almost complete specimen; P6554, the visceral surface of the skull roof; and four other incomplete specimens, P5474, P6572, P56113a, b and P56115a, b. P6577a is probably *P. acadicus*, and possibly also P6573d and P6577d.

Specimens showing only thoracic plates: P6576, P7083, P56131, P56137 and RSM GY 1897.51.123, 124, 128.

REMARKS. *Batteraspis fulgens* Pageau 1969, known only by an incomplete AL, may well be a separate species of *Phlyctaenius* (Denison 1978: 60). I have not included it in the formal synonymy since I have not had the opportunity to examine the specimen at first hand.

Phlyctaenius atholi (Pageau 1969)

Figs 5B; 6; 7C, D; 9B; 11B; 12D; 16B, E; 17A; 18B

1888 *Coccosteus acadicus* Whiteaves; Whiteaves: 94; pl. 9, fig. 2.
1890*b* *Phlyctaenius acadicus* (Whiteaves) Traquair: pl. 3, fig. 2.
1892*b* *Phlyctaenaspis acadica* (Whiteaves) Woodward: 481.

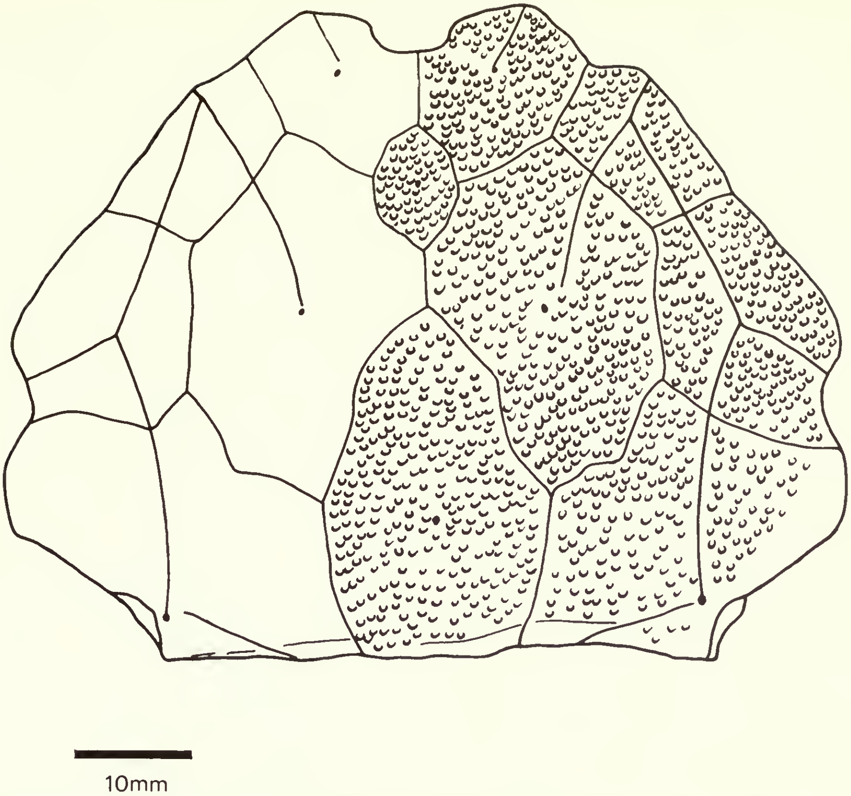


Fig. 6 *Phlyctaenius atholi* (Pageau). Restoration of skull roof based on the lectotype, RSM GY 1897.51.123.

1916	*Phlyctaenaspis acadica* (Whiteaves); Chapman: pl. 21, fig. 6.
1933	*Phlyctaenaspis acadica* (Whiteaves); Heintz: pl. 3, fig. 1.
1969	*Phlyctaenaspis atholi* Pageau: 819; pl. 25, fig. 2; pl. 28, fig. 5; text-fig. 19.1, 4.

Diagnosis (emended). Species of *Phlyctaenius* in which the skull roof breadth at the level of the M is greater than the PrO–PNu length; 100 B/L index = 110–142 (excluding RP); posterolateral margin of PNu divided by an angle into two sections; ornament tubercles uniformly arranged; tubercles large with rounded peaks; growth centre of PNu inside posterolateral margin of plate and fairly close to posterior margin; occipital cross-commissural groove on PNu clearly indicated; postoccipital para-articular process on PNu well developed; infraorbital sensory canals converging strongly anteriorly; anterior point of Nu approximately in line with growth centres of Cs; Nu length greater than half PrO–PNu length of skull roof; AL equidimensional; ADL with prominent posterior process above lateral line groove.

Lectotype. Pageau based *P. atholi* upon two skull roofs (Pageau 1969, specimens RSM GY 1897.51.113, 123) but he did not specify which was the holotype. I therefore here select as **lectotype** the better-preserved specimen, RSM GY 1897.51.123, a skull roof from the Lower or Middle Devonian, Campbellton, New Brunswick, Canada. Fig. 5B.

Horizon and locality. Latest Lower or earliest Middle Devonian, Campbellton, New Brunswick, Canada.

Material. Specimens showing skull roofs: nine fairly complete specimens; P6556, P6573a, P6573g, P6574, a (part and counterpart), P56120, RSM GY 1887.20.44a, RSM GY 1897.51.113, 123, RSM GY 1978.30.3. Also five others which are poorly preserved.

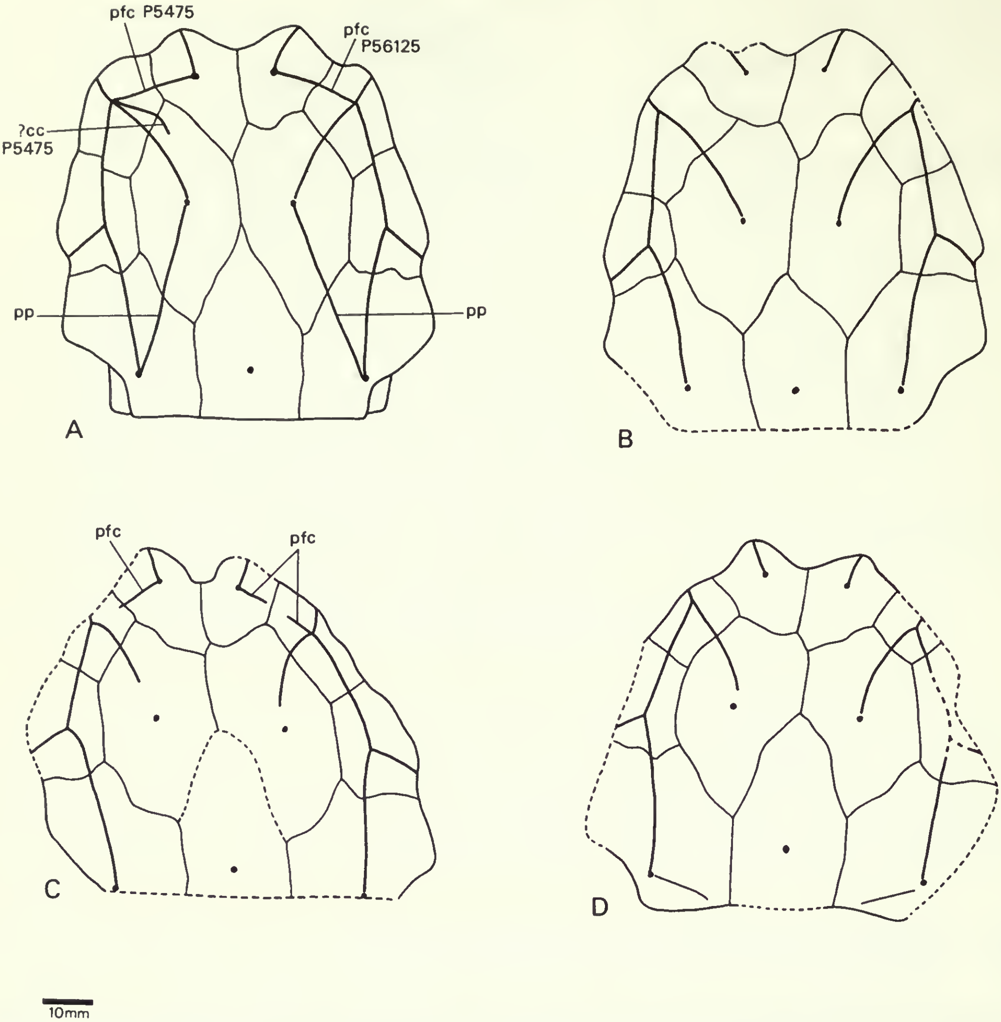


Fig. 7 Outline of skull roofs showing variations of sensory lines and suture lines C/PrO in *P. stenosus* and *P. atholi*. A. *P. stenosus* sp. nov. with sensory line variations: pp – posterior pit line grooves after RSM GY 1897.51.118; pfc – profundus pit line grooves after P56125, P5475; cc – central canal duplication after P5475. B. *P. stenosus* sp. nov. (RSM GY 1887.20.44). C. *P. atholi* with sensory line variation: pfc – profundus pit line grooves after RSM GY 1978.30.3. D. *P. atholi*: C/Nu suture tends to curve towards the C (RSM GY 1887.20.44a) in contrast to conditions in other species.

Specimens showing only thoracic plates: P6559, P6575e, P6577e, h, P56126b, P56127, RSM GY 1887.20.45, RSM GY 1897.51.126, 130, 131, 132, 142, 143, RSM GY 1978.30.8, 12, 13.

REMARKS. Pageau (1969: 820) specified three characters in erecting this species:

1. Ornament of large, uniformly arranged tubercles with rounded peaks;
2. RP not attached to skull roof; and
3. Presence of a median postpineal.

The first of these characters is valid but the remaining two are omitted from the emended diagnosis presented here, for the following reasons.

The detachment of the RP is not a distinguishing character since skull roofs without attached RP elements are also known for both *P. acadicus* and *P. stenosus*. In RSM GY 1897.51.113, 123 and P6556 a median postpineal is present. This plate is hexagonal (Figs 5, 6) with the smallest tubercles, indicating the growth centre, at the centre of the plate. However, a number of specimens which do not possess this plate are similar to *P. atholi* in all other characters by which they were compared, and group with that species in a multivariate analysis (see p. 3). On these specimens, where the postpineal is absent, the suture line pattern between the PrOs and Cs is very variable in *P. atholi* as it is in *P. stenosus* (Fig. 7), and the right or left PrO may extend between the two Cs (RSM GY 1887.20.44a, RSM GY 1978.30.3). Denison (1958:507) remarked that the PrO, and possibly the R, P and PNs, '. . . show the most variable development of any of the dermal bones of the arctolepid cranial roof', and that this may be 'an indication of the relative plasticity of the anterior part of the skull'. Miles & Westoll (1968: 390) commented that in *Coccosteus* 'the pineal region is by far the most variable part of the dermal bone-pattern', although they never found a separate postpineal 'in any of the several hundred individuals of *C. cuspidatus* examined' or, indeed, in any other coccosteomorph. They conclude that 'differential growth rates of the bones from their radiation centres is considered sufficient to explain all observed conditions . . .'. Species closely related to *Phlyctaenius*, such as *Heightingtonaspis anglica* (Traquair) (White 1961, 1969) and *Aggeraspis heintzi* (Gross) (Gross 1962) sometimes show a postpineal between the PrO and C. I also note considerable variation in the presence or absence of small roofing bones in *Acipenser* (Jarvik 1948), *Eusthenopteron* (Jarvik 1944), dipnoans (Miles 1977) and *Osteolepis* (Graham-Smith 1978b). It is concluded that the presence of a postpineal is an individual variation rather than a distinguishing character of *P. atholi*.

The figures and description by Pageau (1969) of the skull roof and several thoracic plates of *Gaspeaspis cassivii* Pageau from the Battery Point formation, Gaspé Bay, Quebec suggest that this species should be considered a synonym of *P. atholi*. I have not included it in the formal synonymy since I have not examined the material at first hand. Pageau specified two characters for *Gaspeaspis cassivii*, the form of the sub-paranuchal depression on the visceral surface of the skull roof and the superficial ornament. The visceral surface of the PNu of *P. atholi* is unknown and this first character cannot be compared. The superficial ornament of *G. cassivii* is of large, uniformly distributed tubercles with rounded peaks. This is a character of *P. atholi* (compare Pageau 1969: pl. 28, fig. 5, *P. atholi*, with his pl. 27, fig. 2, *G. cassivii*). There are also several other points of similarity from which I infer that these species are conspecific:

1. The breadth of the skull roof at the M is considerably greater than the length (Pageau 1969: pl. 27, fig. 2; pl. 28, figs 1, 2);
2. The posterolateral margin of the PNu is divided by an angle into two sections (Pageau 1969: pl. 28, fig. 2);
3. The postoccipital para-articular process on the PNu is well developed (Pageau 1969: pl. 28, fig. 2); and
4. The infraorbital sensory canals tend to converge anteriorly (Pageau 1969: pl. 27, fig. 2; pl. 28, fig. 1).

Phlyctaenius stenosus sp. nov.

Figs 5C; 7A, B; 8; 9C; 11C; 12C; 13; 14; 15; 16A, C, F; 17B–F; 18A, C–E

1888	*Coccosteus acadicus* Whiteaves; Whiteaves: 94; pl. 9, fig. 4.
1890*b*	*Phlyctaenius acadicus* (Whiteaves) Traquair: pl. 3, fig. 1.
1891	*Phlyctaenaspis acadica* (Whiteaves) Woodward: 296.
1892*a*	*Phlyctaenaspis acadica* (Whiteaves); Woodward: pl. 1, fig. 7.
1907	*Phlyctaenaspis acadica* (Whiteaves); Whiteaves: pl. 4, figs 1, 2.
1925	*Phlyctaenaspis acadica* (Whiteaves); Stensiö: text-fig. 21.
1933	*Phlyctaenaspis acadica* (Whiteaves); Heintz: 128; text-figs 1, 2, 3 (in part), 4, 5 (in part), 6 (in part); pl. 1, figs 1–4; pl. 3, figs 2, 3.
1958	*Phlyctaenaspis acadica* (Whiteaves); Denison: text-figs 105G, 106D, 108B, 109A, 111A, 114A.
1969	*Phlyctaenaspis acadica* (Whiteaves); Pageau: 814.
1969	*Phlyctaenaspis acadica* (Whiteaves); Miles: 147; text-fig. 9h.

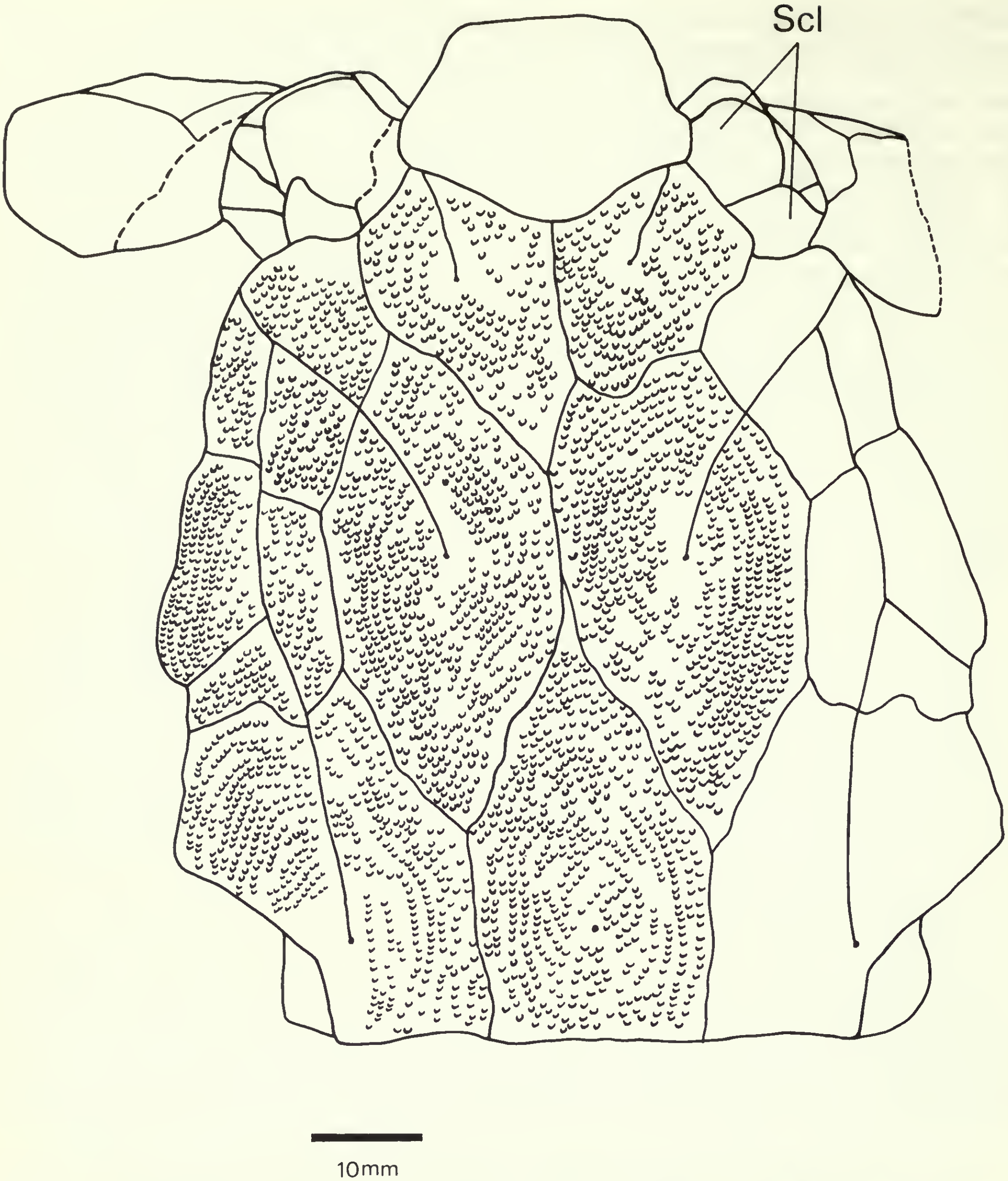


Fig. 8 *Phlyctaenius stenosus* sp. nov. Restoration of skull roof based on the holotype P6555 and P56125 and P56116a. Scl – sclerotic plates.

DIAGNOSIS. Species of *Phlyctaenius* in which the skull roof breadth at the level of the M is equal to, or a little less than, the PrO–PNu length; 100 B/L index = 90–99 (excluding RP), posterolateral margin of PNu marked by an internal angle; anterior and lateral margins of RP gently concave; sutures evident; ornament tubercles form regular concentric rows parallel to the plate margins; tubercles generally medium-sized with sharp to rounded peaks; growth centre of PNu inside posterolateral margin of plate and fairly close to posterior margin; postoccipital para-articular process on PNu well developed; infraorbital canals subparallel, or converging anteriorly; anterior point of Nu posterior to growth centres of C; Nu length less than half PrO–PNu length of skull roof; AL equidimensional.

NAME. *Stenosus* is from the Greek *στενός*, narrow, in reference to the most striking feature of this species, the narrowness of the skull roof at the level of the M and the PNu.

HOLOTYPE. P6555, a skull roof, Lower or Middle Devonian, Campbellton, New Brunswick, Canada. Fig. 5C.

HORIZON AND LOCALITY. Latest Lower or earliest Middle Devonian, Campbellton, New Brunswick, Canada.

MATERIAL. Specimens showing skull roofs: holotype P6555, P5475, P5972, P6573h, P6573i, P56114a, b, P56116a, b, P56117a, b, P56121, P56122, P56123, P56125, RSM GY 1887.20.44, RSM GY 1897.51.118, RSM GY 1897.51.125, RSM GY 1898.180.24, RSM GY 1978.30.5, RSM GY 1978.30.7; and possibly P6573e, P56124.

Specimens showing only thoracic plates: P5973, P6559a, c, P6577b, d, P56126a, b, P56131, P56134, P56142, P56144, P56146, P56148, P60900, RSM GY 1897.51.120, 121, 134, 135, 136, 139, 140, RSM GY 1978.30.10, 11.

Comparative description

This section is intended to supplement and amplify the information included in the species diagnoses and accompanying remarks.

The plates forming the skull roof of *Phlyctaenius* are normal for arthrodires. They are strongly sutured together, except for the PM, of which a fragment is questionably identified on P6577a, here referred to *P. acadicus*. As with other primitive (non-brachythoracid) arthrodires the orbital notches are shallow, the sutures show very little overlap, the Cs are hexagonal and the Nu is parallel-sided and anteriorly wedged between the Cs. The shape and proportions of the head shield and constituent plates, particularly the Nu and PNu, vary between the three species. These differences are best seen by comparing Figs 4, 5, 6 and 8.

The suture lines are clearly visible on the ornamented surface in *P. stenosus* (Figs 5C, 8), normally visible on *P. atholi* (Figs 5B, 6) and are not evident on *P. acadicus* (Figs 5A, 4), where the path of the sutures is deduced from the ornament pattern, and, on the visceral surface, by the junctions of radiating lines (Figs 5D, 10). The dorsal surface immediately adjacent to the posterior margin of the skull roof of *P. acadicus* is unornamented and bevelled and was probably covered with skin. The skull roof specimens of *Phlyctaenius* have been flattened in preservation. A paper model of the thoracic shield was made by restoring to best fit drawings of individual plates. This suggests that in life the head showed a marked transverse curvature, the highest point coinciding with the growth centre of the Nu. From here ridges run to the growth centre of each C thus delimiting a dorsal flattened triangular area. From the sides of this area the skull roof slopes laterally. The RP (not known in *P. atholi*) differs in *P. acadicus* and *P. stenosus*. In the former the anterior and lateral margins are convex (Figs 4, 5A) while in the latter these margins are gently concave (Figs 5C, 8) and where they meet the resulting corners turn downwards – a feature noted by Heintz. Heintz (1933: 130) also noted indistinct impressions on P6555, here referred to *P. stenosus*, as evidence of nasal apertures. However, nasal apertures were not recognized in the specimens studied. The limit between the R and P components of the RP is obvious in *P. acadicus* where there is a clear break in the ornament (RSM GY 1897.51.129) and a suture line on the visceral surface (P6554), but in *P. stenosus* the ornament is continuous.

The shape of the PrO appears highly variable in *Phlyctaenius*, particularly along the contact with the C (p. 13) and there may be marked asymmetry in this region of the roof of *P. stenosus* (Fig. 7A, B) and *P. atholi* (Fig. 7C, D). The variation in this region of the skull roof is discussed more fully on p. 13. The anterior margin of the PrO of *P. atholi* is strongly concave (Figs 5B, 6) and this contrasts with the more gently concave anterior margin of the PrO of *P. acadicus* (Figs 4, 5A) and *P. stenosus* (Figs 5C, 8).

Towards the posterior end of the head shield further differences between the three species are seen in the shape of the PNu (Figs 4, 5A–D, 6, 8). The posterior margin meets the lateral margin at varying angles: between 40° and 50° in *P. acadicus*, between 60° and 77° in *P. atholi*, 90° in

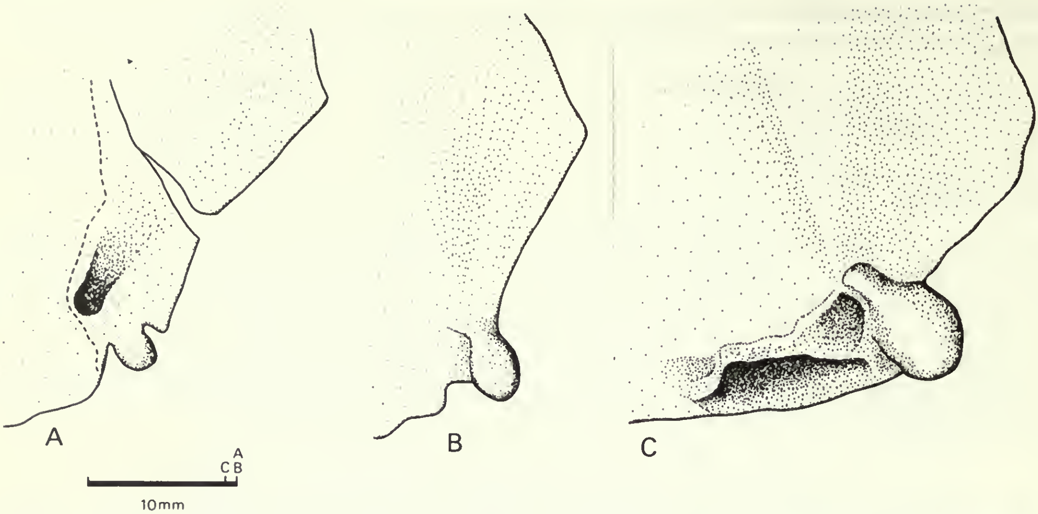


Fig. 9 Different development of the para-articular process on the visceral surface of the PNu in the three species of *Phlyctaenius*: A. *P. acadicus* (Whiteaves), P6554. B. *P. atholi* (Pageau), P6573b. C. *P. stenosus* sp. nov., RSM GY 1898.180.24.

P. stenosus. Beneath the surface of the PNu the cranial division of the craniothoracic joint is seen as the development of a para-articular process and a glenoid fossa which receives the trochlear of the ADL. The relative sizes of the process differ in the three species and are best seen in Fig. 9. Of particular diagnostic significance is the margin of the dorsal ornamented surface above the joint, where it shows a marked inside angle in *P. stenosus* and *P. atholi* absent in *P. acadicus* (Figs 4, 5A–C, 6, 8).

A cucullaris depression was recognized on one specimen (P6554, *P. acadicus*) showing the visceral surface, and is similar to that described for *Buchanosteus* by Young (1979: fig. 2). A pineal foramen is only recognized in one specimen of *P. stenosus* (P6555) and the broken margin suggests that it was quite small. The visceral surface of the skull roof of *P. acadicus* (P6554, P6572) suggests that both a pineal fontanelle within the neurocranium and a shallow pineal pit in the visceral surface of the P are developed.

The external opening for the endolymphatic duct is only recognized in *P. atholi* (RSM GY 1887.20.44a); this occurs just mesial to the growth centre of the PNu. Although an opening for the endolymphatic duct was not recognized in *P. acadicus* it is possible that the duct ran for some distance through the PNu. In RSM GY 1897.51.129 this is indicated by a slight linear indentation which runs from a point mesial to the growth centre of the PNu to the C/PNu/Nu junction (Figs 4, 5A). It may have been formed by the collapse of the roofing bone of the duct (D. Goujet, personal communication).

Little evidence of the neurocranium is preserved, as with '*Phlyctaenius*' sp. (Gross 1937: pl. 2, fig. 10; text-fig. 21q). Stensiö (1925: 165) suggested that this indicates that the neurocranium was either entirely cartilaginous or only slightly ossified. The outline of the neurocranium in *P. acadicus* is evident as the boundary between two types of surface on the underside of the skull roof and by the surface relief. Specimen P6554 shows the outline most clearly (Fig. 10) but remnants occur on several other specimens. Where present the outline appears to be generally similar in all three species of *Phlyctaenius*. The bone surface which must have lain beyond the limits of the neurocranium is dark-coloured, smooth and with few canals for blood vessels and nerves. It is present around the skull roof margins. The surface which originally lay above the neurocranium is lighter in colour, uneven and marked by numerous grooves. The radiating growth pattern of the individual dermal plates is very clear (Figs 5D, 10). This surface is covered in places by a thin layer of lighter-coloured bone with a shiny, uneven surface. This might

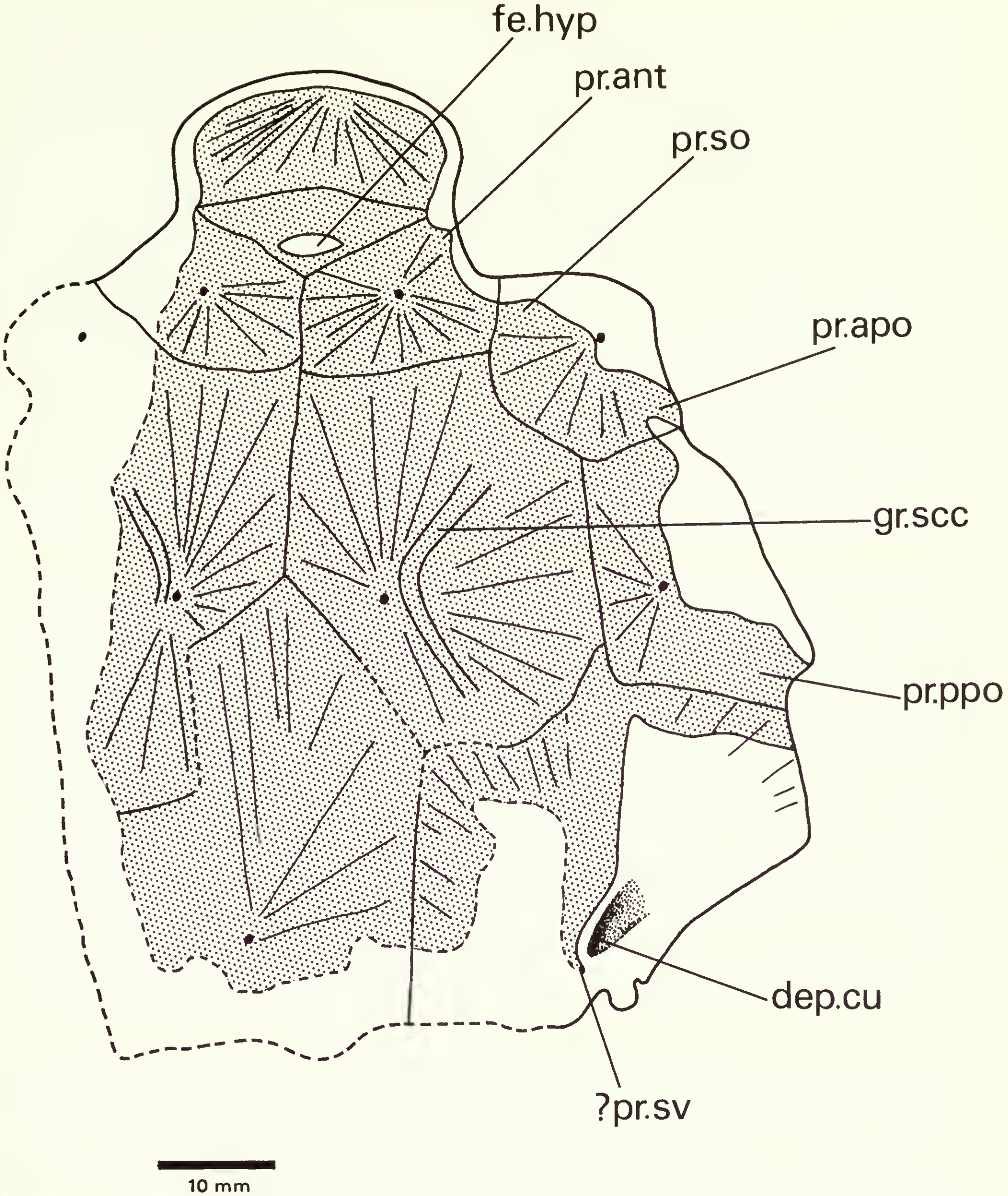


Fig. 10 *Phlyctaenius acadicus* (Whiteaves). Visceral surface of skull roof showing area covered by neurocranium (P6554). The path of the sutures is deduced from the junctions of radiating lines. dep.cu – cucullaris depression; fe.hyp – hypophysial fenestra; gr.scc – groove for semicircular canal; pr.ant – antorbital process; pr.apo – anterior postorbital process; pr.ppo – posterior postorbital process; pr.so – supraorbital process; ?pr.sv – possible supravagal process. Scale bar 10 mm.

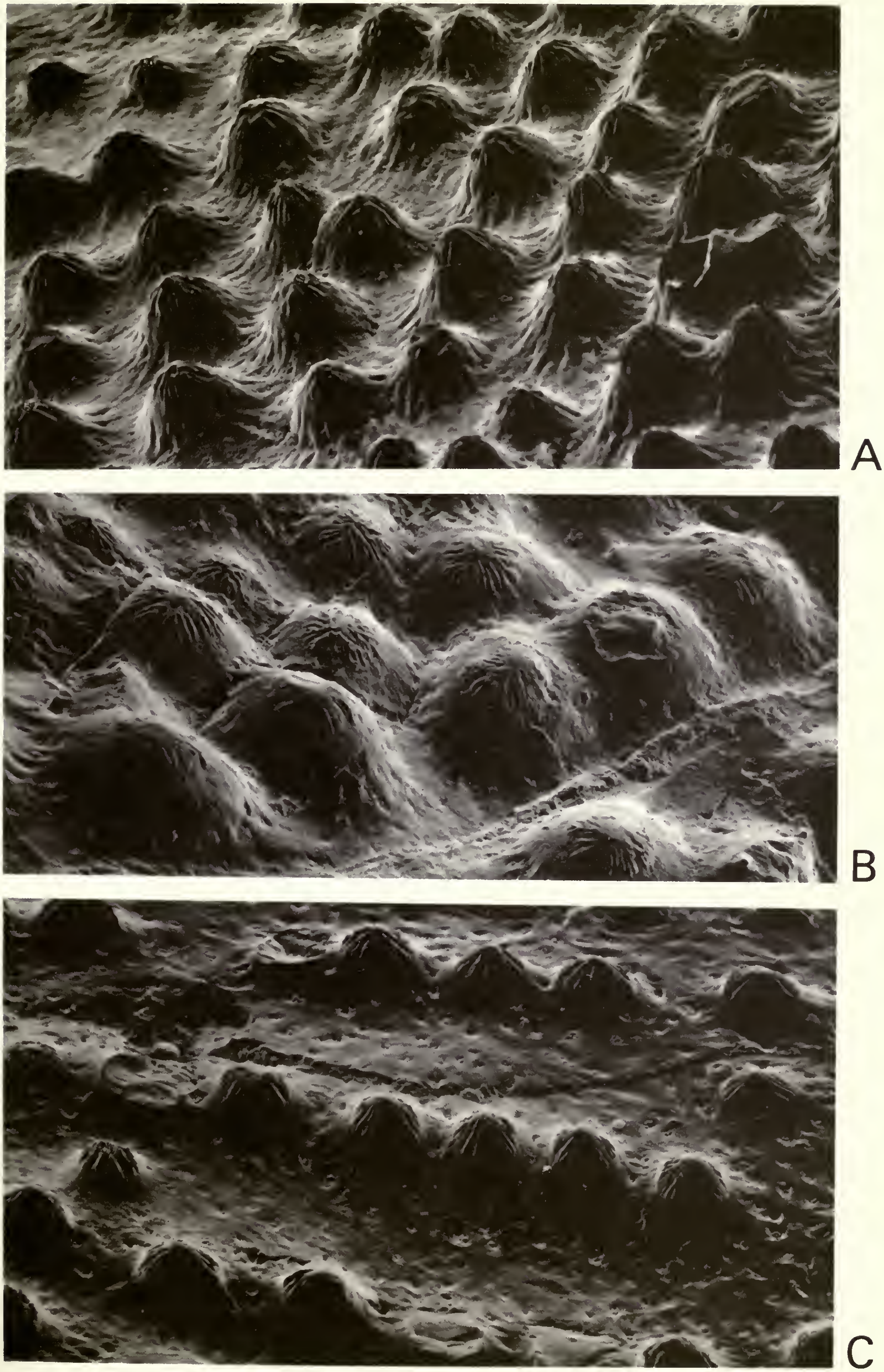
represent isolated areas of perichondral ossification. Denison (1978: 59) comments that '. . . the neurocranium . . . of *Phlyctaenius* . . . is perichondrally ossified'. The original source is Ørvig (1951: 408; pl. 7, fig. 1), where he says that the endocranium of *P. acadicus* is ossified to a large extent, and has a lining consisting of thin perichondral bone, and a thin basal layer of globular calcified cartilage. He goes on to say that the skull roof bone has fused with the perichondral bone layer of the dorsal endocranial wall beneath the growth centres. However, perichondral bone was not certainly recognized in the material examined here.

The RP is often detached from the remainder of the skull roof in all three species studied here (in *P. acadicus* it is detached in two out of six suitable specimens, in *P. stenosus* in 13 out of 14 suitable specimens and in *P. atholi* in all eight suitable specimens). This suggests that the nasal capsules were units independent of the orbital and occipital region of the neurocranium. This type of neurocranium would seem to belong to Stensiö's (1963: 820) 'type B' group. The dorsal outline of the postethmo-occipital portion of the neurocranium differs in many respects from the reconstruction of that of *P. acadicus* provided by Stensiö (1925: text-fig. 20). It is broader, has more processes and a wider occipital region (Figs 5D, 10). The postethmoidal region is generally similar in outline to that of *Kujdanowiaspis* (Stensiö 1945, 1963), though it differs in details. It is broad throughout. The remaining fragments of the occipital region indicate that it appears to be wider than in *Actinolepis magna* (Mark-Kurik 1973: fig. 7a, b), and *Kujdanowiaspis* (Stensiö 1945, 1963). The antorbital, supra-orbital, anterior and posterior postorbital and possibly supravagal processes are developed (Fig. 10). Between the antorbital and supra-orbital processes is a notch for the orbital recess. The anterior postorbital process is situated at the PtO/M suture, and the posterior postorbital process at the M/PNu suture. The latter process does not bifurcate as it does in *Kujdanowiaspis* (Stensiö 1945, 1963), *Actinolepis* (Mark-Kurik 1973: fig. 7a, b) and *Dicksonosteus* (Goujet 1975: fig. 4). However, the impression left by this process ends abruptly at the lateral margin of the skull roof, between the M and the PNu. It may well bifurcate beneath the PM as in *Actinolepis* (Mark-Kurik 1973: fig. 7a, b), although no evidence of the neurocranium is indicated on the fragment of the PM of specimen P6577a.

Specimen P56120 is here identified as *P. atholi*; although poorly preserved it has several interesting features. Impressions are present for the infra-orbital and lateral sensory canals, and impressions of a number of other canals are preserved. From a comparison with those of *Kujdanowiaspis rectiformis* (Brotzen) (Stensiö 1945: fig. 1) they can be interpreted: antero-laterally there are dorsal canals for cutaneous nerves and vessels, lateral to the growth centres of the Cs there are canals for a dorsal branch of the glossopharyngeal and vessels, and postero-laterally canals for a supratemporal branch of the vagus and for vessels. Other canals are indistinct on this specimen.

The general pattern of sensory lines on the skull roof is seen in Figs 4, 5A–C, 6, 8. In *P. stenosus* the infraorbital canals run nearly parallel to one another while in the other two species they converge anteriorly, particularly in *P. atholi*. Several specimens of *P. stenosus* show variations in the sensory canals: paired posterior pit-line grooves, not normally identified in *Phlyctaenius*, occur on specimen RSM GY 1897.51.118 (Fig. 7A). Each occurs as a paired row of tubercles extending between the growth centres of the C and PNu. In many actinolepids and phlyctaeniids posterior pit-lines are not evident, or are indicated as short grooves near to the growth centres of the C and the PNu (e.g. *Simblaspis, Sigaspis, Arctolepis*; Denison 1978: text-figs 31, 38). A posterior pit-line is evident on *Actinolepis* extending between the growth centres of the C and the PNu (Denison 1978: text-fig. 31). Posterior pit-lines may occur as discontinuous grooves between the growth centres of the C and the PNu of brachythoracids such as *Holonema, Buchanosteus, Millerosteus, Coccosteus* and *Dicksonosteus* (Denison 1978: text-figs 45, 49, 57). Specimen P5475, *P. stenosus*, has a short groove which runs from the growth centre of the PtO to the PtO/C border, which may be a short duplication of the central canal (Fig. 7A). Although not typical of *Phlyctaenius*, shallow traces of grooves, which may be profundus pit-line grooves, run between the growth centres of the PrOs and PtOs of *P. stenosus* (P5475; P6573i; P56125, Fig. 7A). This is also seen in one specimen of *P. atholi* (RSM GY 1978.30.3, Fig. 7C). Profundus grooves occur in some other actinolepids (e.g. *Bryantolepis brachycephalus* and *Simblaspis cachensis* Denison, 1958: 508). Graham-Smith (1978*a*: 26) suggests that 'profundus' grooves in some dolichothoracids may be produced as a result of an extension of the suborbital canal becoming anchored ontogenetically to a rudiment of the PtO.

Fig. 11 *Phlyctaenius*, ornament tubercles: A. *P. acadicus* (Whiteaves) (RSM GY 1897.51.129) × 22, SEM SP5/407. B. *P. atholi* (Pageau) (RSM GY 1897.51.123) × 25, SEM SP5/428. C. *P. stenosus* sp. nov. (P6573h) × 25, SEM SP5/415.


A
B
C

In some specimens of *P. stenosus* (P6555, P56125, P5972) the suture line between the PtO and the M on one side of the infraorbital canal is displaced relative to that on the other side (Figs 7A, 8). In each case the section of the suture line lateral to the infraorbital canal is more anterior than the mesial section. Similar displacement at the junctions of sensory canal grooves has been figured by Gross (1941: text-fig. 7a) for several species of *Bothriolepis*, and Graham-Smith (1978*a*: 23–25) has proposed an explanation of how this may have occurred.

The occipital cross-commissural groove is seen in *P. acadicus* and *P. atholi* where it runs from the growth centre of the PNu posteromesially to notch the posterior margin about half-way along. It is possible that the path of this groove may indicate the presence of extrascapular plates, as suggested by Miles & Dennis (1979: 45). However, extrascapular plates were not seen in any species of *Phlyctaenius*.

The ornament of *Phlyctaenius* is of individual tubercles, the shape, size and arrangement of which differ among the three species (Fig. 11A–C). In each species the ornament tubercles of individual plates are smallest around the growth centre and largest at the plate margins. Tubercles are uniformly arranged and are close together in *P. acadicus*, and normally uniformly arranged in *P. atholi*. In *P. stenosus* they are arranged in rows parallel to the plate margins. Thus it is usually possible to distinguish the approximate outlines of the plates in the three species. In all three species tubercles lateral to the infraorbital sensory canal are smaller than those mesial. In several areas of specimen RSM GY 1897.51.129 it seems that tubercles have overgrown earlier tubercles. This feature was noticed in *P. acadicus* by Gross (1957: pl. 6, fig. 7), and by Ørvig (1957: fig. 9a) who figured a section of *P. acadicus* which shows two generations of tubercles separated by a thin layer of laminar bone. In *Arctolepis magna* Mark-Kurik tubercles often overgrow other tubercles so that 'the concentric arrangement of the tubercles is often considerably confused' (Mark-Kurik 1973: 97).

SOs (Fig. 12C, D) occur on P6555 (*P. stenosus*) and as isolated fragments of *Phlyctaenius* sp., RSM GY 1897.51.118 and 126. Areas missing, due to fracture, from specimen P6555 are present

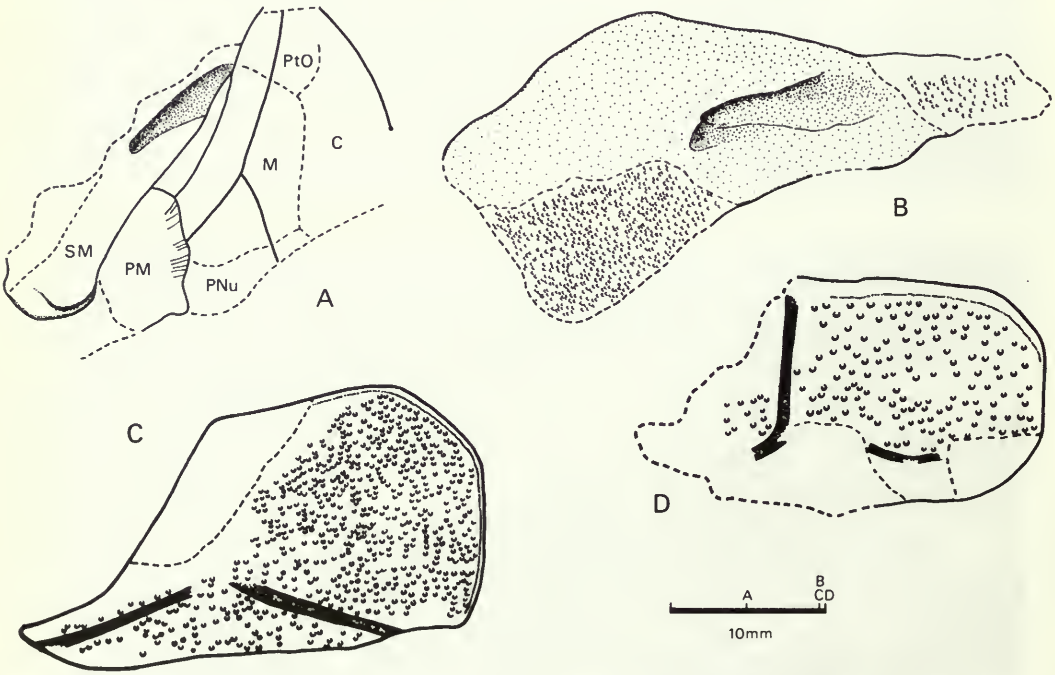


Fig. 12 Cheek plates of *Phlyctaenius*. A. *P. acadicus* (Whiteaves), fragments of SM and PM, P6577a. B. *P.* sp. SM showing groove for hyomandibular, P6573d. C. *P. stenosus* sp. nov., SO, holotype P6555. D. *P. atholi* (Pageau), SO, RSM GY 1897.51.126.

on the isolated fragments of the SO (Fig. 12D). In section the SO may be divided into two laminae which lie at an angle to one another (Heintz 1933: fig. 1). The bend between the two laminae runs horizontally across the 'blade' to the orbital margin. The postorbital branch of the infraorbital canal has not previously been recorded for *Phlyctaenius* but it is present in RSM GY1897.51.118 and 126, and in each it runs in usual arthrodire fashion (Fig. 12D). A post-suborbital was not found.

The sclerotic plates (Fig. 8, Scl) occur as fragments on specimen P6555, *P. stenosus*, where there are apparently four on each side, as is usual for arthrodires (Denison 1978: 2). Each is thick and strongly arched, similar to those of *Arctolepis* (Heintz 1962: 36–38). Heintz (1933: 130) commented that 'the sclerotic ring in *Phlyctaenaspis* must form something like a more or less strong capsule protruding from the orbital opening of the head roof'. The sclerotic plates of Placodermi are sometimes ornamented (Denison 1978: 2; *Arctolepis*, Heintz 1962: 36–38), and the outer surface of those of *Phlyctaenius* have an ornament of uniformly arranged tubercles. Heintz (1933: 129) commented on the presence of fragments of possible PNs occurring near the orbit on P6555. However, they are poorly preserved and cannot be positively identified.

The remains of three isolated gnathal elements are recognized (Heintz 1933: pl. 2, figs 2–4). All three are poorly preserved, fractured and incomplete. Two are believed to be inferognathals, and one a superognathal, and are believed, by association, to belong to *P. stenosus* (RSM GY1897.51.125), and *P. atholi* (RSM GY1897.51.126). The inferognathal elements (RSM GY1897.51.125, 126) are small and slender and consist of an anterior tooth-bearing section and a posterior blade, without teeth. RSM GY1897.51.126 is narrow posteriorly, becoming wider anteriorly. On the tooth-bearing section of this specimen about 25 to 30 teeth are evident. In both elements the teeth are of varying sizes, are conical and tend to become larger towards what is presumed to be the anterior end. Broken sections confirm Heintz' (1933: 132) comment that the teeth appear to have no pulp cavity.

Other cranial elements of *Phlyctaenius* are preserved as fragments. Four poorly-preserved specimens are identified as submarginals (Fig. 12A, B): P6577a (Heintz 1933: pl. 2, fig. 1), P6573d – both *P. acadicus*; RSM GY1897.51.125 – *P. stenosus*; RSM GY1897.51.118 – *Phlyctaenius* sp. All plates show the visceral surface and show small traces of ornament as impression. The first two specimens mentioned show a shallow longitudinal groove anteriorly which probably represents the point of attachment for the hyomandibular.

A small fragment of the visceral surface of a plate, possibly a PM, is attached to the margin of the skull roof of P6577a, *P. acadicus* (Fig. 12A herein and Heintz 1933: pl. 2, fig. 1) and an impression of the visceral surface of the PM is present on P5972, *P. stenosus*. The outline of the impression is indistinct.

Specimens of the thoracic shield of *Phlyctaenius* are represented mostly as isolated plates, although some occur in association and a few with a skull roof. The ornament of individual plates may be matched, in most cases, with one or other of the three types of skull roof ornament.

Previous restorations of the trunk shield of *Phlyctaenius* (Heintz 1933) were based upon information from more than one species. The present reconstruction of the thoracic shield (Figs 13, 14, 15) is based upon *Phlyctaenius stenosus* since, of the three species, the specimens of this show the most complete series of thoracic plates. The reconstruction was difficult because of variation in size, and the incompleteness of many of the individual plates, and because associations of trunk plates from one individual are rare and never complete. The reconstruction was done by making outline tracings of individual plates. The size of the tracings was adjusted with the Grant Projector to relate to those of one of the more complete associations of plates belonging to a single individual. The relative sizes of the overlap areas were taken into consideration. The resulting composite plate outlines were traced onto thin card, cut out individually, and from these the thoracic shield was reconstructed.

The ventral surface of the thoracic shield is flat with the remaining plates forming an arch. Sections vertically through the thoracic shield show an anterior triangular cross section and a posterior seven-sided section, similar to those described and figured by Heintz (1933: 141, fig. 5).

The mutual relationships of constituent plates is that typical of primitive arthrodires (Denison

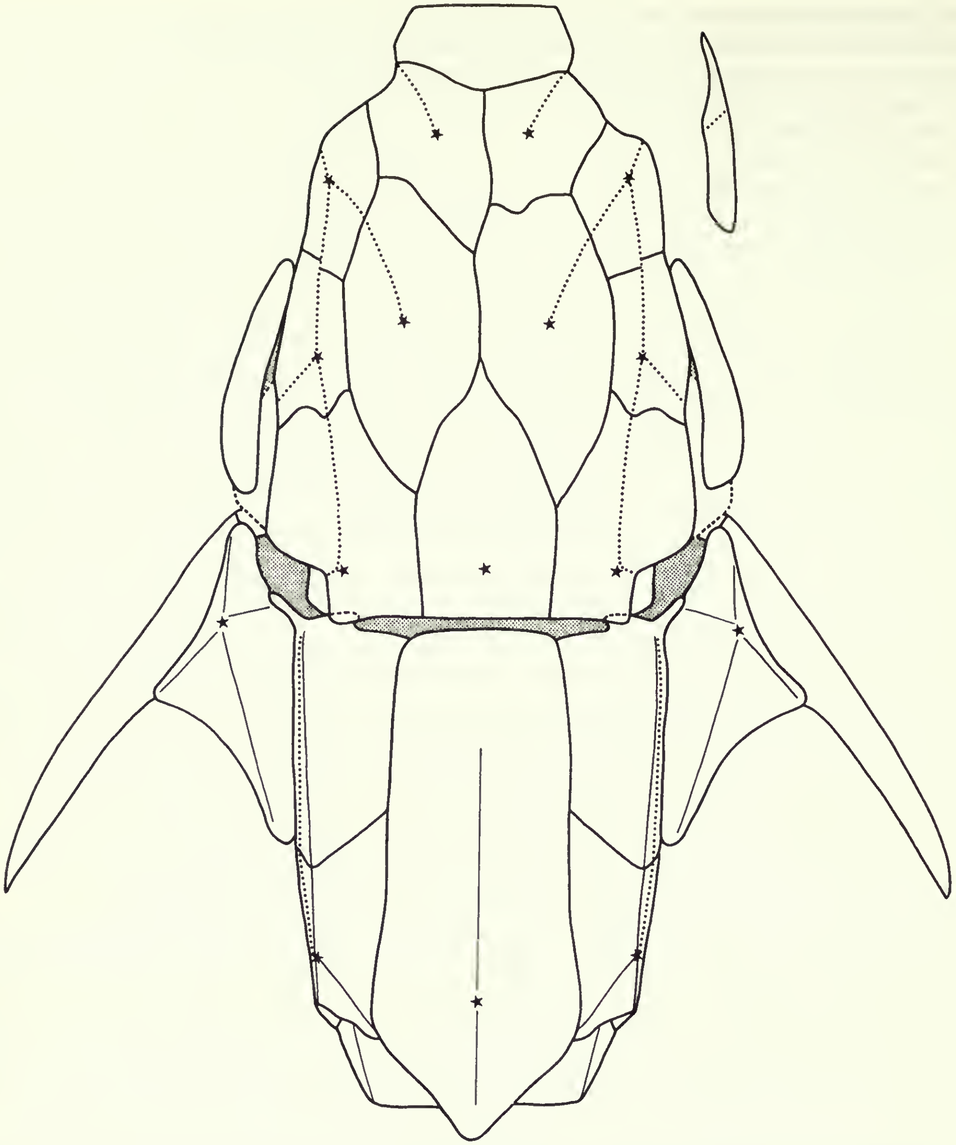


Fig. 13 *Phlyctaenius stenosus* sp. nov. Restoration of skull roof and trunk shield in dorsal view. The SO is drawn separately since its exact position is unknown. The sensory lines are dotted and the growth centres starred.

1950, 1978), in which the PL and PVL contact one another to enclose a pectoral fenestra. However, the extent of the overlap areas of constituent plates suggests that the margin of the pectoral fenestra is bounded by the AVL, AL and possibly the PVL (Figs 13, 14). There is a well-developed 'Dorsolateralkante' and 'Ventrolateralkante' (Gross 1932) and a postbrachial lamina on the AVL and PVL.

The differences between the thoracic shields of the three species are most conspicuous in the shapes of the MD, AL and ADL. The MD of *P. stenosus* (Figs 13, 16A) shows a square anterior end in contrast to the rounded margin in *P. atholi* (Fig. 16B). In both, there is a low dorsal crest (more developed in *P. stenosus*) and the visceral surface shows a small median ridge which might

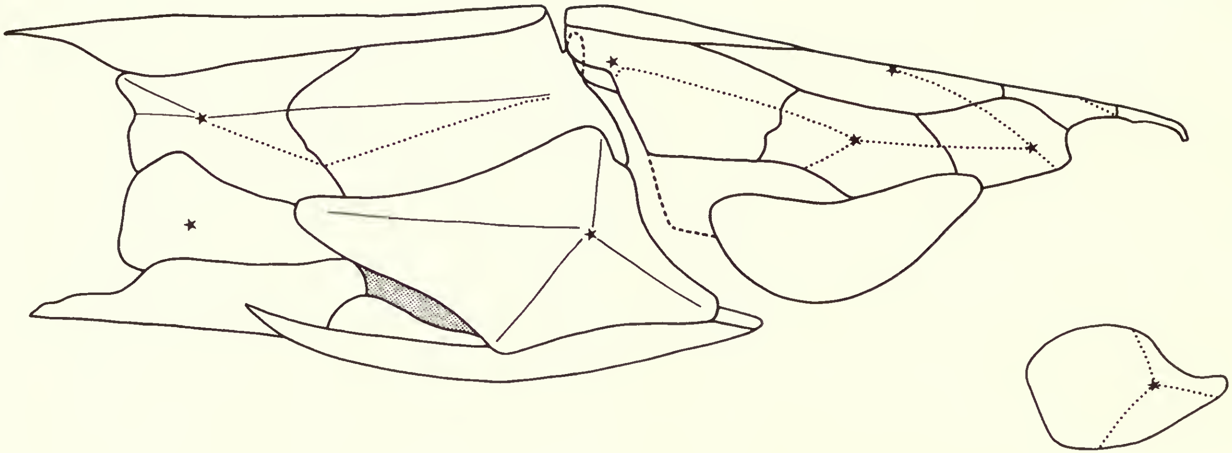


Fig. 14 *Phlyctaenius stenosus* sp. nov. Restoration of skull roof and trunk shield in lateral view. The SO is drawn separately since its exact position is unknown. The sensory lines are dotted and the growth centres starred.

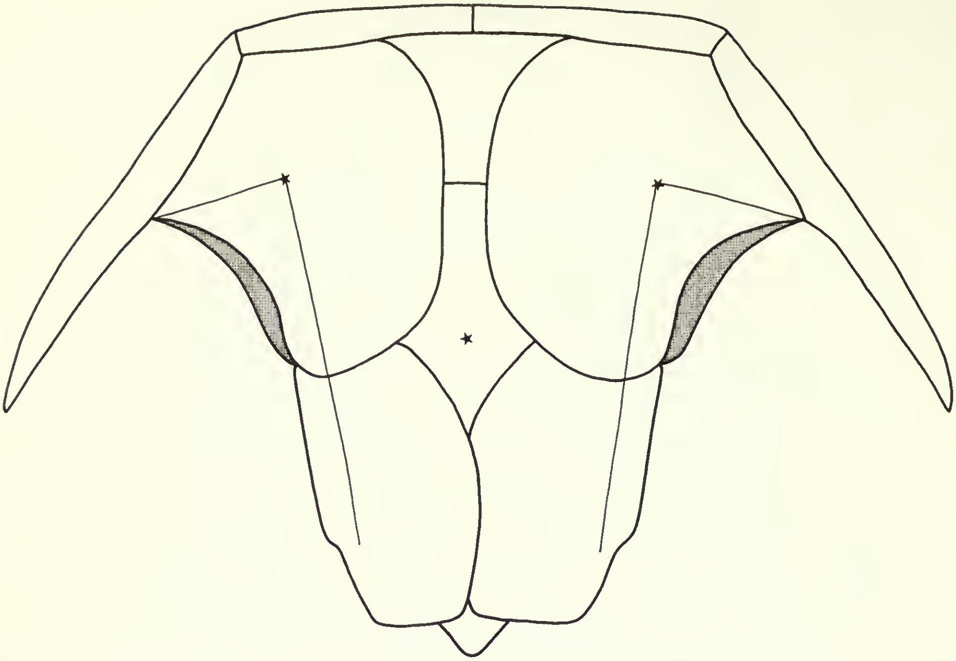


Fig. 15 *Phlyctaenius stenosus* sp. nov. Restoration of trunk shield in ventral view. The growth centres are starred.

be interpreted as a rudimentary keel. Only one specimen (RSM GY 1897.51.128) of the MD of *P. acadicus* was examined and this was too poorly preserved for comment.

The ADL is known in *P. atholi* (Fig. 17A) and *P. stenosus* (Figs 14, 17B, C). Both show an articular condyle below which there is, in *P. stenosus*, a swollen anterior margin resembling an obstantic process, although it is not as well developed as that process in *Holonema* (Miles 1971: 158). Similarly, there is no obvious development of a para-articular face but the shape of the matching angle of the paranuchal suggests that there must have been some articulation with the ADL ventrolateral to the articular condyle articulation. Specimens of the visceral surface of the ADL include: RSM GY 1897.51.124, 125, 126; P6575; P56143. The specimens are incomplete and it is not possible to identify them to species by their outline. On these specimens the swollen process running from below the articular condyle anteroventrally is very prominent as a ridge along the anterior margin of the lower lamina of the plate, and is similar to the 'ventral ridge' on the ADL of *Holonema* (Miles 1971: text-fig. 68). It borders the upper part of the anterior margin of the AL (Figs 13, 14, 17A–C). There appears to be a small para-articular face of rough-surfaced bone on the visceral surface of RSM GY 1897.51.125 and P56143. The differences in shape of the ADL of *P. atholi* and *P. stenosus* are seen in Fig. 17A–C. In both, the plate is divided by a pronounced ridge beneath which the lateral line groove runs to notch the posterior margin. The main lateral line is continued as a groove as far as the growth centre of the PDL of both *P. stenosus* (Figs 14, 17D, E) and *P. atholi*; thereafter it does not mark the bone (cf. Heintz 1933: fig. 3). The PDL of these two species (unknown for *P. acadicus*) is very similar except that the groove for the lateral line is not accompanied by a ridge in *P. atholi* as it is in *P. stenosus*. The PDL of *P. stenosus* is interesting in showing a small triangular area posteriorly in which the arrangement of the tubercular ornament differs from (P56126a, b), or is similar to (P6577d, Fig. 17E), that on the rest of the plate.

I thank Dr Gavin Young for drawing my attention to an unusual PDL figured and described by Pageau (1969: 819; pl. 30, fig. 10; fig. 21M; specimen LTC-29D in Laboratoire Teilhard de Chardin, Univ. Québec, Montreal). The specimen is from a horizon yielding specimens of

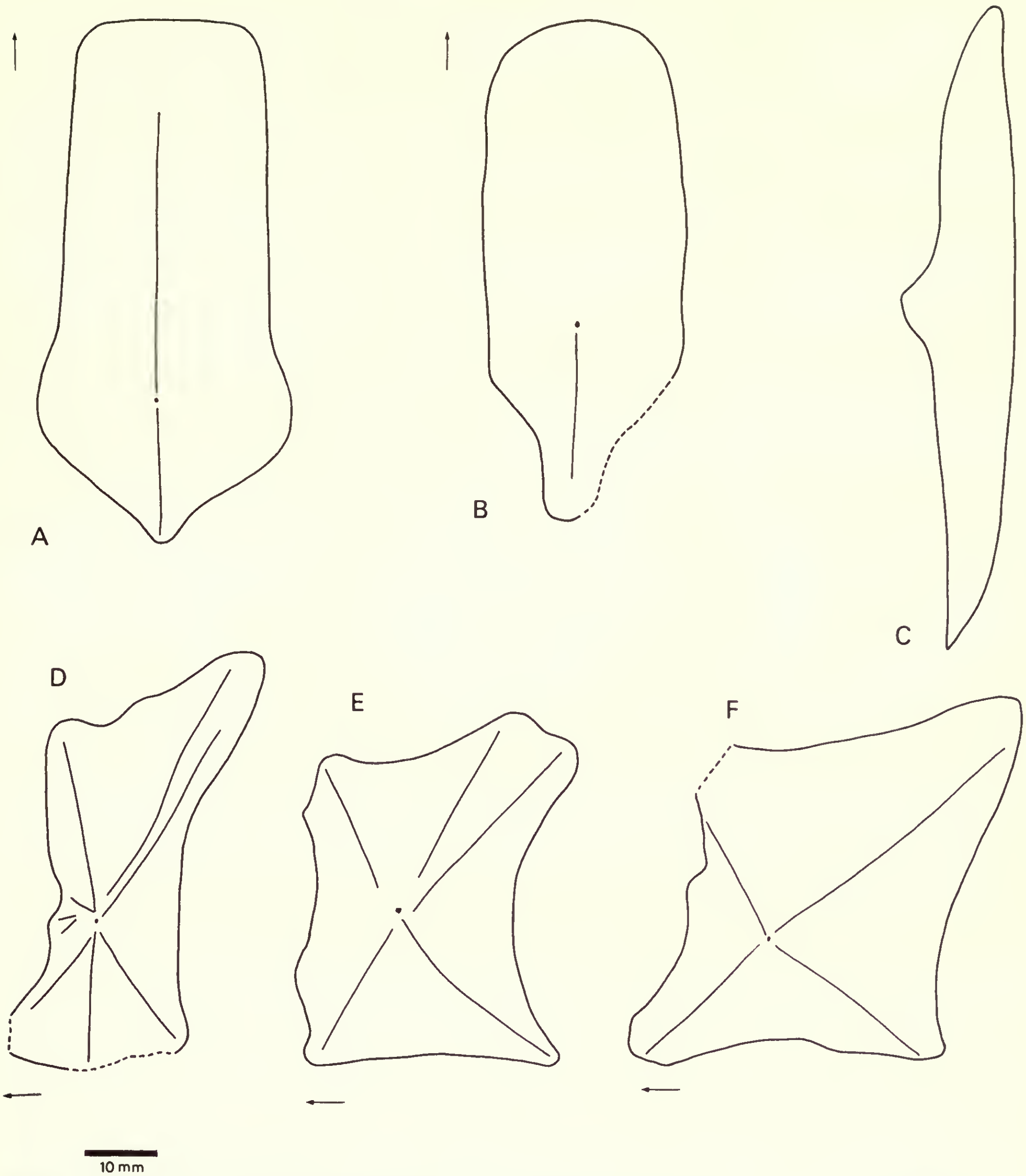


Fig. 16 *Phlyctaenius*, isolated thoracic plates to show shape differences between species. MD: A. *P. stenosus* sp. nov. (based on RSM GY 1978.30.10 and P56131); B. *P. atholi* (Pageau) (RSM GY 1897.51.132); Sp: C. ? *P. stenosus* sp. nov. (RSM GY 1897.51.137); AL: D. *P. acadicus* (Whiteaves) (P6576); E. *P. atholi* (Pageau) (P6577e, h – drawing reversed); F. *P. stenosus* sp. nov. (P56144, RSM GY 1897.51.120, 121). Arrow indicates anterior.

Phlyctaenius acadicus and has ornament similar to *Phlyctaenius* (*P. stenosus*). Pageau provisionally identified the PDL as *P. acadicus*. However, the specimen is short and is unlike any of the specimens of PDLs of *Phlyctaenius* studied here (Figs 14, 17D, E).

The AL is known for all three species and comparative outlines are given in Fig. 16D–F, from which it may be seen that the AL of *P. acadicus* is very tall and narrow with a short spinal margin. This contrasts with the relatively long plate of *P. stenosus*; *P. atholi* is intermediate in these dimensions. The posterodorsal corner of the AL of *P. atholi* is distinctive in being truncated. As

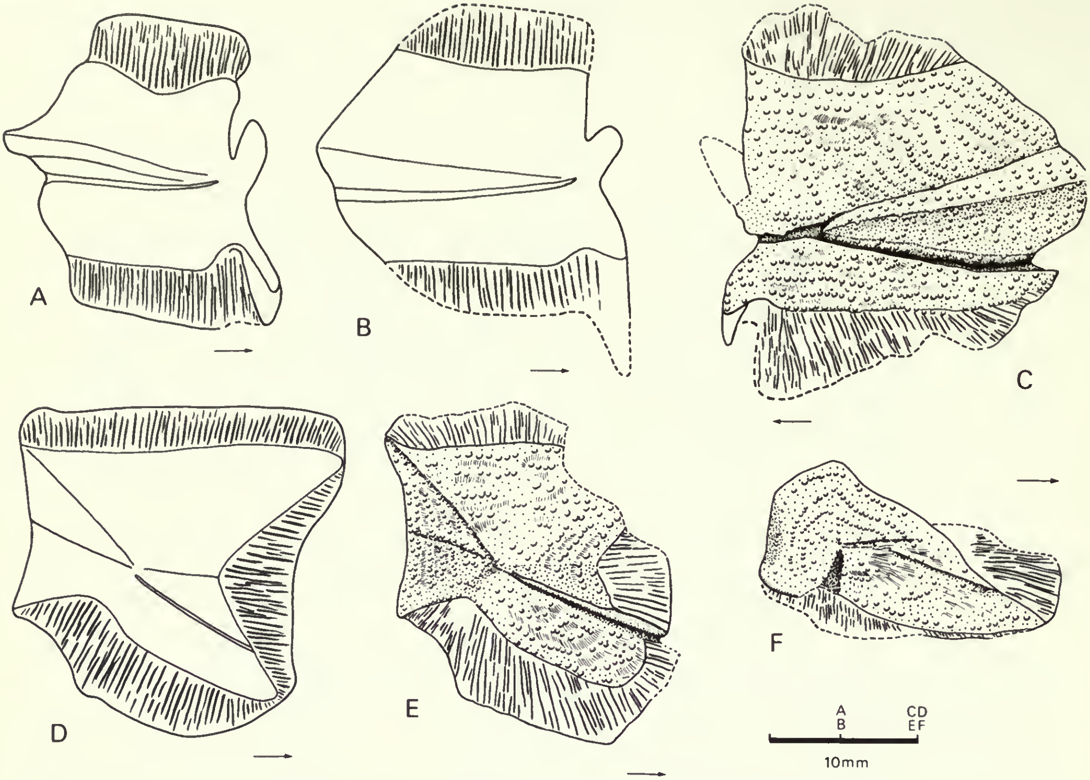


Fig. 17 *Phlyctaenius*, isolated thoracic plates to show shape differences between species. ADL: A. *P. atholi* (Pageau) (based on RSM GY 1978.30.13); B. *P. stenosus* sp. nov. (based on P56142 and P6577d); C. *P. stenosus* sp. nov. (P6577d). PDL: D. *P. stenosus* sp. nov. (based on P6577d and P56126a, b); E. *P. stenosus* sp. nov. (P6577d). PL: F. *P. stenosus* sp. nov. (P6577d). Arrow indicates anterior.

is usual in primitive arthrodires the AL is divided into four quadrants by ridges and the pattern of ornament may vary considerably over the surface of the plate (Heintz 1933: fig. 4).

The outline of the AVL of the three species discussed here is shown in Figs 15, 18A, B, where the differences in proportion can be seen. Particular points of distinction are the width of the AVL in *P. acadicus* associated with the short and divergent spinal margin. The AVL of *P. atholi* is relatively narrow, with *P. stenosus* intermediate in proportion. The ornament on the AVL is very variable but is most completely seen in specimens of *P. stenosus*. It is of interest to note that the side of the plate immediately bordering the subpectoral emargination is heavily ornamented with tubercles, usually uniformly arranged. This is unlike the AVL of *Coccosteus* (Miles & Westoll 1968: 434) and *Barrydalaspis* (Chaloner *et al.* 1980: 131), where tubercles are absent immediately adjacent to this margin. Impressions of the scapulocoracoid are indicated on the visceral surface of several AVLs, and are approximately similar in outline to that of *Barrydalaspis theroni* (Chaloner *et al.* 1980: fig. 3).

Spinals are generally poorly preserved. The shape, which appears constant for all three species, may be seen in the restoration of *P. stenosus* (Figs 13–15) and in Fig. 16C. The spinal of *P. stenosus* is the best known. The ornament over the inner and central areas is of small- to medium-sized tubercles. These may be rounded or elongated, sometimes forming rows parallel, or slightly inclined, to the longitudinal axis of the plate; occasionally they are uniformly arranged. The outer margin of the plate is covered by larger tubercles. Although Heintz (1933: 138) commented that spines were not evident on either the inner or outer margins of the Sp, small spine-like projections, possibly modified tubercles, are present on the inner margin of P6576b

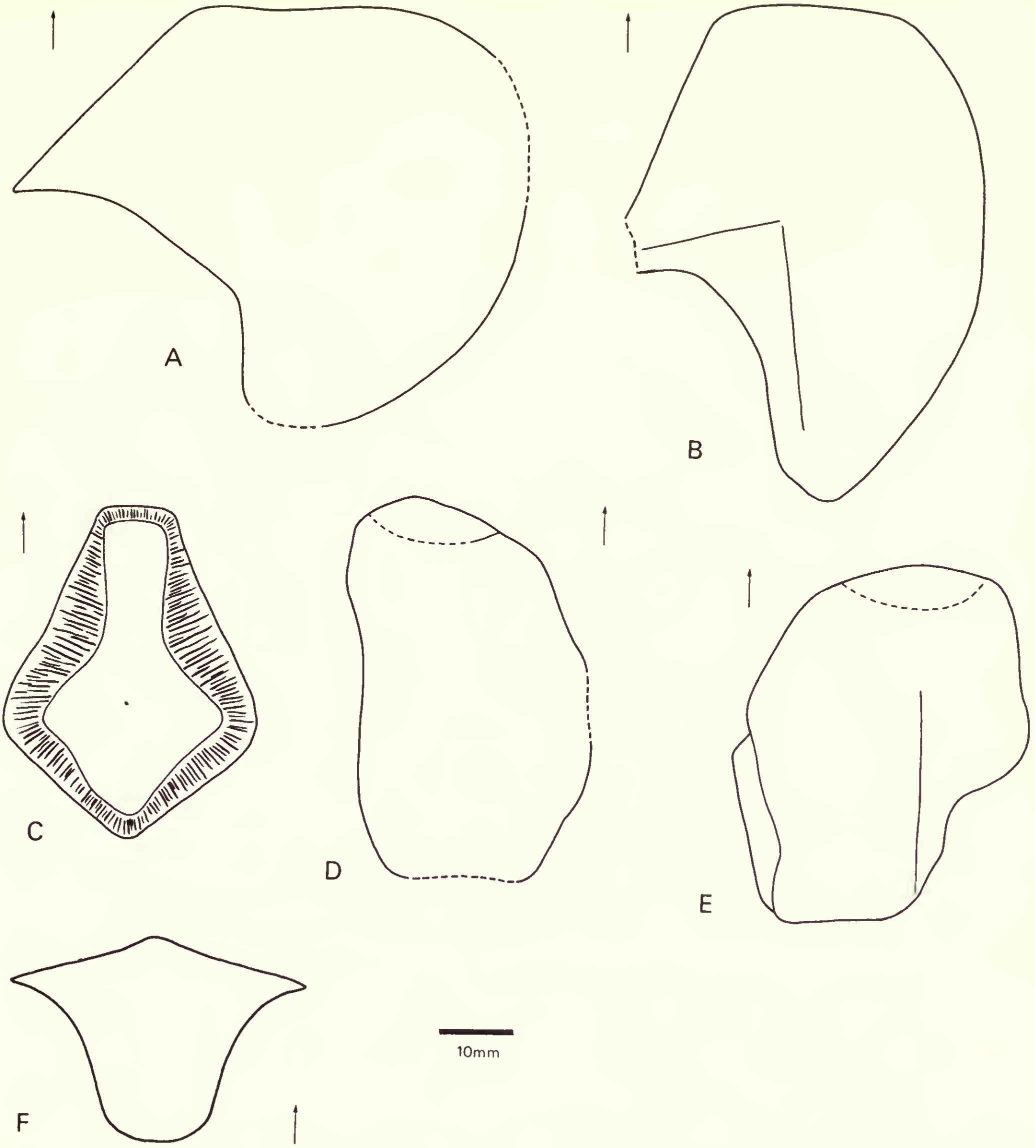


Fig. 18 *Phlyctaenius*, isolated thoracic plates. AVL: A. ? *P. acadicus* (Whiteaves) (RSM GY 1897.51.123); B. ? *P. atholi* (Pageau) (P56126b). PMV: C. *P. stenosus* sp. nov. (P56126a, b). PVL: D. *P. acadicus* (Whiteaves) (P56131); E. *P. stenosus* sp. nov. (RSM GY 1897.51.118). AMV: F. *P. acadicus* (Whiteaves) (P6577a). Arrow indicates anterior.

and RSM GY 1897.51.134. Specimen P6576 is possibly that figured by Heintz (1933: figs 3, 5, 6). It is relatively small and short. Small tubercles occupy the centre of the plate, and larger tubercles the outer margin. The plate is situated close to an AL assigned to *P. acadicus* and may belong to this species.

The IL is very incompletely known. Several specimens (RSM GY 1897.51.134–136) of *P. stenosus* displaying this bone show that the ventral surface is narrow (Fig. 15) and has a rounded recess for the AMV towards the mid-line. A mesial section of the IL is present on RSM GY 1897.51.134 and two laminae of the IL, set at an angle to each other, seem to be indistinctly indicated. What little of the surface ornament is preserved seems to be of uniformly arranged tubercles.

Heintz (1933: 142) recognized four kinds of scales:

1. Rhomboidal or quadrangular scales without evidence of overlap margins, and with typical *Phlyctaenius*-like ornament.
2. '. . . more or less oblong triangular scales with clearly overlapping margins along both the longitudinal sides . . .'. They are strongly arched and thick.
3. '. . . fulcra-like quite big scales . . . bent along the longitudinal axis with a deep incut in the hind margin'.
4. '. . . quite large, thin roundish scales . . . on the outside covered with concentrically arranged tubercles.'

The rhomboidal or quadrangular scales on RSM GY 1897.51.128 (Heintz 1933: pl. 3, fig. 6a) are situated close to an MD of *P. acadicus*, and probably belong to this species. Scales which are similar, though subtriangular or round, are also present in this area. The long, narrow, triangular scales figured by Heintz (1933) are associated with plates of *P. stenosus* (Heintz 1933: pl. 3, fig. 5) and an MD of *P. acadicus* (Heintz 1933: pl. 3, fig. 6b). At each of the longer margins of the scales on RSM GY 1897.51.125 is a narrow, sloping lateral surface which may be overlap surface. Heintz comments that the scales are ornamented with large tubercles (Heintz 1933: pl. 2, figs 6, 7), though this is not clear on the specimens he described. These scales resemble the flank scales of *Sigaspis* (Goujet 1973), which are tall and narrow and overlap one another. It is possible that the tall narrow scales on RSM GY 1897.51.125 and 128 are flank scales of *P. stenosus* and *P. acadicus*. The 'fulcra-like' scales, examples of which were described and figured by Heintz (1933: pl. 3, fig. 4: P6559b, an isolated scale, and fig. 5, lower right corner of his photograph: RSM GY 1897.51.127, 128) are believed to be dorsal ridge scales. The ornament is of *P. acadicus* type. The scale is heart-shaped, conical and deep in section. Its deepest point is at the growth centre. At its wider end is a V-shaped opening with rounded edges extending from the growth centre to the scale margins. On specimens RSM GY 1897.51.127 and 128 two dorsal ridge scales, which are mentioned by Miles (1969: 132), are present, associated with an MD of *P. acadicus* and a large cluster of scales. Both specimens are fractured and compressed. The outlines are indistinct and the V-shaped notch is not seen. It seems that the pointed end of the scale is anterior. Heintz (1933: pl. 3, fig. 3; P7084) figured a '. . . quite large, thin, roundish scale' or 'plate . . . covered with concentrically arranged tubercles'. This specimen is believed to be a C of *P. stenosus*.

In addition to the scales described above two further varieties are recognized. Small round or ellipsoidal scales are situated close to the thoracic shield of P6577a, *P. acadicus*, and possibly belong to this species. There is no evidence of overlap surfaces or ornament. Also a small, round scale, about 8 mm in diameter and ornamented with concentrically arranged tubercles, is associated with small, presumed juvenile, thoracic plates of *P. stenosus* (P6577a), and may belong to the same individual. Two ridges diverge from the central growth centre to the margin of the scale. This specimen is believed to be a median ridge scale, and may be a juvenile, or a different variety of that described above.

Discussion

Traditional classifications of *Phlyctaenius* (often as *Phlyctaenaspis*: see pp. 5, 10) have been provided by Woodward (1891), Zittel (1895, 1932), Fowler (1947), Denison (1958, 1975), Obruchev (1964, 1967), Miles (1969, 1973) and Stensiö (1969). Woodward (1891) and Zittel (1895) placed *Phlyctaenius* in the family Coccosteidae; later Woodward *in* Zittel (1932), followed by Obruchev (1964, 1967) and Miles (1973), placed the genus in the family Phlyctaenaspidae; Fowler (1947), followed by Denison (1978), placed it in the family Phlyctaeniidae. Stensiö (1969) placed *Phlyctaenius* in the order Dolichothoraci.

In attempting to reconstruct the phylogeny of arthrodires Miles (1969), Stensiö (1969) and Denison (1975) identified evolutionary trends in order to establish characters by which taxa could be grouped. Miles (1969) divided the arthrodires into four main groups, which he recognized as grades of taxa at a particular level of biological organization, each successively more 'biologically efficient' than the last. *Phlyctaenius acadicus* (Whiteaves), representing the phlyctaenaspid level of organization, was regarded as intermediate between the presumed more primitive, actinolepid, and the more advanced, brachythoracid, levels of organization. More recently placoderm interrelationships have been expressed in the form of cladograms, proposed by Denison (1978), Miles & Dennis (1979), Dennis & Miles (1979*a*,*b*, 1980) and Young (1979, 1980, 1981). The cladogram of Denison (1978) is a general cladogram for the Arthrodira. That of Miles & Dennis (1979) and Dennis & Miles (1979*a*,*b*, 1980) (with slight variations) is concerned mainly with the brachythoracid arthrodires. The cladogram of Young (1981) is concerned with phlyctaenioids. The cladograms of Denison (1978) and of Young (1979, 1981) agree generally in the relationships of the Phlyctaeniidae. In all three cladograms the suborders Phlyctaeniina, Heterosteina, Coccosteina and Pachyosteina (Denison 1978: fig. 30), or representative taxa, are grouped together on the possession of a hinged dermal neck-joint. Young (1979, 1981) adds the loss of AV plates (if primitive for placoderms), although Denison (1978: fig. 30) suggests that the presence of paired AVs is a specialization of the Actinolepidae. Miles & Dennis (1979: 43) and Dennis & Miles (1979*a*: 19, 1979*b*: 308) proposed the presence of a ventral ridge on the MD as a phlyctaenioid synapomorphy, but Young & Gorter (1981) reject this since a ventral ridge on the MD is present also in some actinolepids (e.g. *Aethaspis, Sigaspis, Actinolepis*). Denison (1978) separated the suborder Phlyctaeniina, including the families Phlyctaeniidae, Holonematidae and possibly the Williamsaspidae, on the basis of a long, narrow MD. He also suggested that the elongation of the Sps is a specialization of the Phlyctaeniidae. However, as Young & Gorter (1981: 109) remark, neither of these characters is reliable since the Sps of some actinolepids and phlyctaeniids are of similar length; a long narrow MD is also present in some brachythoracids, e.g. *Gemuendenaspis*. They conclude, therefore, that both characters are plesiomorphous and this leaves the Phlyctaeniina without a character. They also recognize that the family Phlyctaeniidae can only be defined on the basis of primitive characters, and cannot therefore be justified as a monophyletic group.

Within the family Phlyctaeniidae Dennis & Miles (1979*a*: 19, 1979*b*: 308, 1980: 47) have proposed a specialization to separate *Phlyctaenius* together with more advanced taxa; the occipital cross-commissure passing off the posterior margin of the PNu. However, this character seems unacceptable since, as Young & Gorter (1981) have commented, in the brachythoracid *Buchanosteus* this sensory groove has the supposed primitive position. As Young & Gorter (1981) conclude, within the family Phlyctaeniidae subgroups do not seem to be readily defined and the family may be a paraphyletic group.

Of the phlyctaeniids (listed by Denison, 1978) some genera may be more closely related to *Holonema* or *Groenlandaspis*. The genera *Huginaspis, Kolpaspis* and *Prosphymaspis*, each known only by trunk plates, resemble *Groenlandaspis* and *Tiaraspis* in having a high trunk shield and a convex, high-crested MD. *Diadsomaspis*, based on trunk plates, resembles *Groenlandaspis* and *Tiaraspis* in the highly arched MD, and it has a holonematid-like ornament of ridges, though unlike *Groenlandaspis* the ADL is narrow. Denison (1978) comments that the head shield of *Arctolepis* resembles those of the Holonematidae in the wide, fused rostral and postnasals, the large pineal separating the PrOs, and in the shape of the Nu. This genus was included by Young (1981: fig. 17) as the sister-group of a group including *Holonema*. Denison (1978: 55) remarks that *Aggeraspis* includes skull roofs and trunk plates which indicate both phlyctaeniid and actinolepid characters, and may include two genera, or 'might represent a derivative of Actinolepidae that had attained some of the phlyctaeniid specializations'. Of the remaining genera of the family Phlyctaeniidae listed by Denison (1978), *Phlyctaenius* may be distinguished from *Arctaspis* and *Svalbardaspis* in the characteristic shield-shape, and wider proportions, at the M and PNu, of the skull roof. The trunk shield of *Heterogaspis* is short and broad compared with that of *Phlyctaenius*, while that of *Neophlyctaenius sherwoodi* Denison is proportionately longer, and shapes of the plates differ from those of *Phlyctaenius* (cf. Figs 13–15 herein with Denison 1950: pl. 2, figs 1, 2; pl. 3, figs 1, 2). The Sp of *Elegantaspis* is very long in comparison with that of *Phlyctaenius*.

However, I have found no unique derived character shared by these genera, and so they cannot form a monophyletic group. The best known species of the Phlyctaeniidae is *Dickso-*

nosteus arctica Goujet. The general shape of the skull roof and pattern of plates is similar to those of *Phlyctaenius*, although *D. arcticus* is more slender overall. The widths of the skull roof at the levels of the rostral and of the occipital are about equal in *D. arcticus*, contrasting with the condition in *Phlyctaenius* where the rostral region is narrower. The lateral margin of the skull roof of *Phlyctaenius* gently narrows anteriorly at the level of the M and PtO, contrasting with that of *D. arcticus* where it is strongly indented. The R of *Phlyctaenius* is relatively narrower than that of *D. arcticus* and the P is shorter. The PNus of *Phlyctaenius* are wider than those of *D. arcticus*, and the PrO/C margins slope posteromesially, unlike those of *D. arcticus* where they are more transverse. The main differences in the thoracic plates of *Phlyctaenius* and *D. arcticus* concern the MD, Sps and PVLs. The posteriorly pointed MD of *Phlyctaenius* differs from the rounded posterior margin of the MD of *D. arcticus*. The Sps of *D. arcticus* are more slender and curved than those of *Phlyctaenius* and have distinct spines on their inner surface. The mutual PVL overlap of *Phlyctaenius* is simple, while in *D. arcticus* each PVL overlaps the other in a complex S-shaped suture.

The other Phlyctaeniidae include *Denisonosteus weejasperensis* Young & Gorter (1981) from the Middle Devonian near Wee Jasper, New South Wales, Australia, and genera described by Pageau (1969) from the Battery Point formation of Gaspé Bay, Quebec. *D. weejasperensis* may be distinguished from *Phlyctaenius* by the shape of the Nu, the convex posterior margin of the skull roof, and by differences in the shapes of some of the thoracic plates (cf. Figs 4, 5, 6, 8, 13, 14, 16, 17 herein, and Young & Gorter 1981: figs 22, 24). In addition to *P. atholi* from Campbellton, Pageau described six new species from beds contemporaneous with material described here, and some comments are necessary. However, I have not examined the material at first hand, and my comments are based solely on published information. Three of the species are based on trunk plates only: *Kolpaspis beaudryi*, based on an MD and other thoracic plates, is more reminiscent of *Groenlandaspis* as discussed above. *Batteraspis fulgens*, known only by an AL plate, may well be a separate species of *Phlyctaenius* (Denison 1978: 60). However, there is little basis for comparison. *Laurentaspis splendida* is based on an MD, PVL and AL, and an isolated C. There is no basis for considering this species to be closely related to *Phlyctaenius*, and Denison (1978: 105) placed it in Arthrodira *incertae sedis*. *Quebecaspis russelli* (renamed by Denison (1978: 59) as *Pageauaspis*) and *Cartieraspis nigra*, each based on a skull roof and isolated thoracic plates, differ from *Phlyctaenius* species in the shapes of some of the skull roof plates, particularly the long, slender Nu. The posterior margin of the PNu of *C. nigra* slopes anterolaterally, unlike that of *Phlyctaenius* where it slopes very gently posterolaterally. The ADL of *C. nigra* is very long and narrow, unlike that of *Phlyctaenius*. *Gaspeaspis cassivii* is based on a skull roof and thoracic plates and, as Denison (1978: 58) remarks, is doubtfully distinct from *Phlyctaenius*. It should probably be considered synonymous with *P. atholi*. The reasons are discussed under *P. atholi* (p. 13).

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British Museum (Natural History)

An account of the Ordovician rocks of the Shelve Inlier in west Salop and part of north Powys

By the late W. F. Whittard, F.R.S. (Compiled by W. T. Dean)

Bulletin of the British Museum (*Natural History*), Geology series
Vol. 33 No. 1. Dec. 1979. 69pp. 38 figs. Large full-colour map

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Taxonomy of the arthrodire *Phlyctaenius* from the Lower or Middle Devonian of Campbellton, New Brunswick, Canada.
By V. T. Young

***Ailsacrinus* gen.nov.: an aberrant millericrinid from the Middle Jurassic of Britain.** By P. D. Taylor

Miscellanea

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Ailsacrinus gen. nov., an aberrant millericrinid from the Middle Jurassic of Britain

P. D. Taylor

Department of Palaeontology, British Museum (Natural History), Cromwell Road, London SW7 5BD

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Synopsis

The genus *Ailsacrinus* is proposed for the millericrinids *A. abbreviatus* sp. nov., from a new Lower–Middle Bathonian locality at Eastington, near Northleach (Gloucestershire), and the established U. Bathonian species *A. prattii* (Gray 1828), known mainly from Lansdown Hill, north of Bath. *Ailsacrinus* is unusual in having a short tapering column, highly variable in length (1–70 columnals), with a rounded distal end. The small calyx contains reduced basals and, in some individuals, an irregular development of accessory plates often with tubercles. Previously undescribed among millericrinids are syzygies in the arms of *Ailsacrinus*, and differentiation of pinnules into an oral series with transversely-ridged pinnulars and a distal series with cover plates. Well-preserved stereom ultrastructure is described in *A. abbreviatus*. The palaeoecology of *Ailsacrinus* is inferred using functional morphological analysis, comparison with living echinoderms, preservational evidence, and facies relationships. Following detachment of the proximal part of the column and crown from the substratum – perhaps quite late in ontogeny – individuals of *Ailsacrinus* probably led a free-living existence. There is some evidence for columnal addition after detachment in *A. abbreviatus*, although not in *A. prattii*, and columnals may have been shed occasionally. Eleutherozoic adults of *A. abbreviatus* seem to have lived in dense interlocking aggregations or mats which would have provided individuals with stability in the absence of grasping cirri, and might also have acted as current baffles to aid suspension feeding. The well-articulated Eastington crinoids were apparently buried catastrophically by shell sand. Although *Ailsacrinus* is presumed to have evolved from an attached millericrinid, the evolutionary trend within the genus is in the opposite direction. Morphological similarities with comatulids may be due to synplesiomorphy or convergence.

Introduction

In 1882 P. Herbert Carpenter published the first full description of the 'Lansdown Encrinite', *Millericrinus prattii* (Gray 1828), an unusual crinoid characterized by a short tapering stem without any obvious means of attachment. Several later authors (Bather 1900, Kirk 1911, Gislén 1934, Ubaghs *et al.* 1978, Roux 1978) used Carpenter's description and reproduced his figures when discussing *M. prattii* as an example of a free-living (eleutherozoic) crinoid belonging to a group otherwise consisting of permanently attached crinoids. It is somewhat surprising, then, that this interesting crinoid has not been re-studied since the time of Carpenter.

Most museum specimens of *M. prattii* were obtained from the Great Oolite of Lansdown Hill, near Bath. However, Carpenter also mentioned apparently conspecific crinoids from Northleach, about 60 km north-east of Bath (Fig. 1). A re-examination of this crinoid was prompted by the discovery of a locality near Northleach which has yielded several hundred well-preserved individuals from rocks of an earlier age than those present at Lansdown. During the study it became apparent that the Northleach and Lansdown crinoids were not conspecific. However, they proved to be sufficiently similar to one another and distinct from established millericrinid genera to warrant their inclusion in a new genus. *Ailsacrinus* gen. nov. is proposed to include the type-species *A. abbreviatus* sp. nov., from Northleach, and *A. prattii* (Gray).

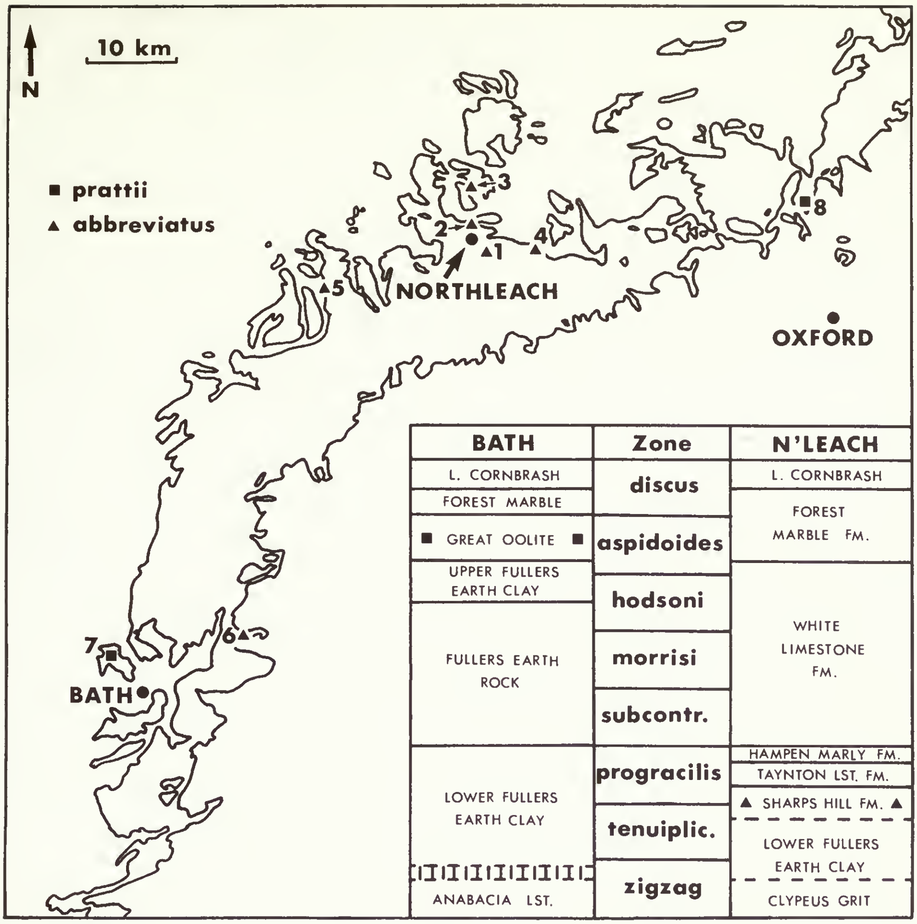
Detailed morphological study of *Ailsacrinus*, as well as corroborating many of Carpenter's observations, has revealed new information relating to arm and pinnule structure and stereom ultrastructure. This has enabled the ontogeny, palaeoecology and phylogenetic affinities of *Ailsacrinus* to be reconsidered.

Specimens studied are in the collections of the British Museum (Natural History) (abbreviated BMNH), the Sedgwick Museum, Cambridge (SM), and the Oxford University Museum (OUM).

Localities

Ailsacrinus abbreviatus

NORTHLEACH AND EASTINGTON. Carpenter (1882) was the first to note the occurrence of the crinoid herein called *A. abbreviatus* in the 'Stonesfield Slate' of Northleach, Gloucestershire. He referred to specimens in the British Museum (Natural History), apparently register numbers 9570, 9572 and 9574 of the Mantell Collection. Other BMNH specimens from Northleach are in



BATH	Zone	N'LEACH
L. CORNBRASH FOREST MARBLE	discus	L. CORNBRASH FOREST MARBLE FM.
■ GREAT OOLITE ■	aspidoides	
UPPER FULLERS EARTH CLAY	hodsoni	WHITE LIMESTONE FM.
FULLERS EARTH ROCK	morrisi	
	subcontr.	
LOWER FULLERS EARTH CLAY	progracilis	HAMPEN MARLY FM. TAYNTON LST. FM.
	tenuiplic.	▲ SHARPS HILL FM. ▲ LOWER FULLERS EARTH CLAY
ANABACIA LST.	zigzag	CLYPEUS GRIT

Fig. 1 Geographical and stratigraphical occurrence of *Ailsacrinus* gen. nov. in southern England. Map shows Bathonian outcrop together with localities for *A. abbreviatus* sp. nov. (triangles numbered 1–6) and *A. prattii* (Gray) (squares numbered 7 and 8). Locality details: 1, new locality near Eastington; 2, Isolation Hospital, Northleach; 3, Notgrove; 4, Windrush; 5, Miserden Park; 6, Corsham; 7, Lansdown Hill; 8, Kirtlington. Stratigraphical details based on Cope *et al.* (1980) modified for Northleach.

the Richardson Collection (E14882–5) and are labelled 'Lower Great Oolite, Quarry near Isolation Hospital'. This is presumably the old quarry described by Richardson (1933: 42) and located north of the town (loc. 2 of Fig. 1).

The newly-discovered locality is a small exposure on a low river cliff near Eastington, 2 km south-east of Northleach (loc. 1 of Fig. 1). Precise locality details have been lodged with the Nature Conservancy Council. Facies comparisons and local geological mapping suggest that the limestone exposed here lies within the Sharps Hill Formation (Sellwood & McKerrow 1974) and its age is likely to be either early Bathonian *tenuiplicatus* Zone or mid-Bathonian *progracilis* Zone (Cope *et al.* 1980). An alternative possibility is that the crinoid bed belongs to the Taynton Limestone Formation (*progracilis* Zone) which is of a similar facies to the Sharps Hill Formation around Northleach. However, this seems less likely because the Taynton Limestone Formation is quartz-deficient, whereas the crinoid bed abounds in quartz. Crinoids occur throughout the thickness (about 26 cm) of the crinoid bed but are most conspicuous on several successive bedding planes (Fig. 2) and tend to be more abundant and better preserved near to the base of the bed. The bed overlies and grades into an oobiosparite and in turn is overlain, with a sharp

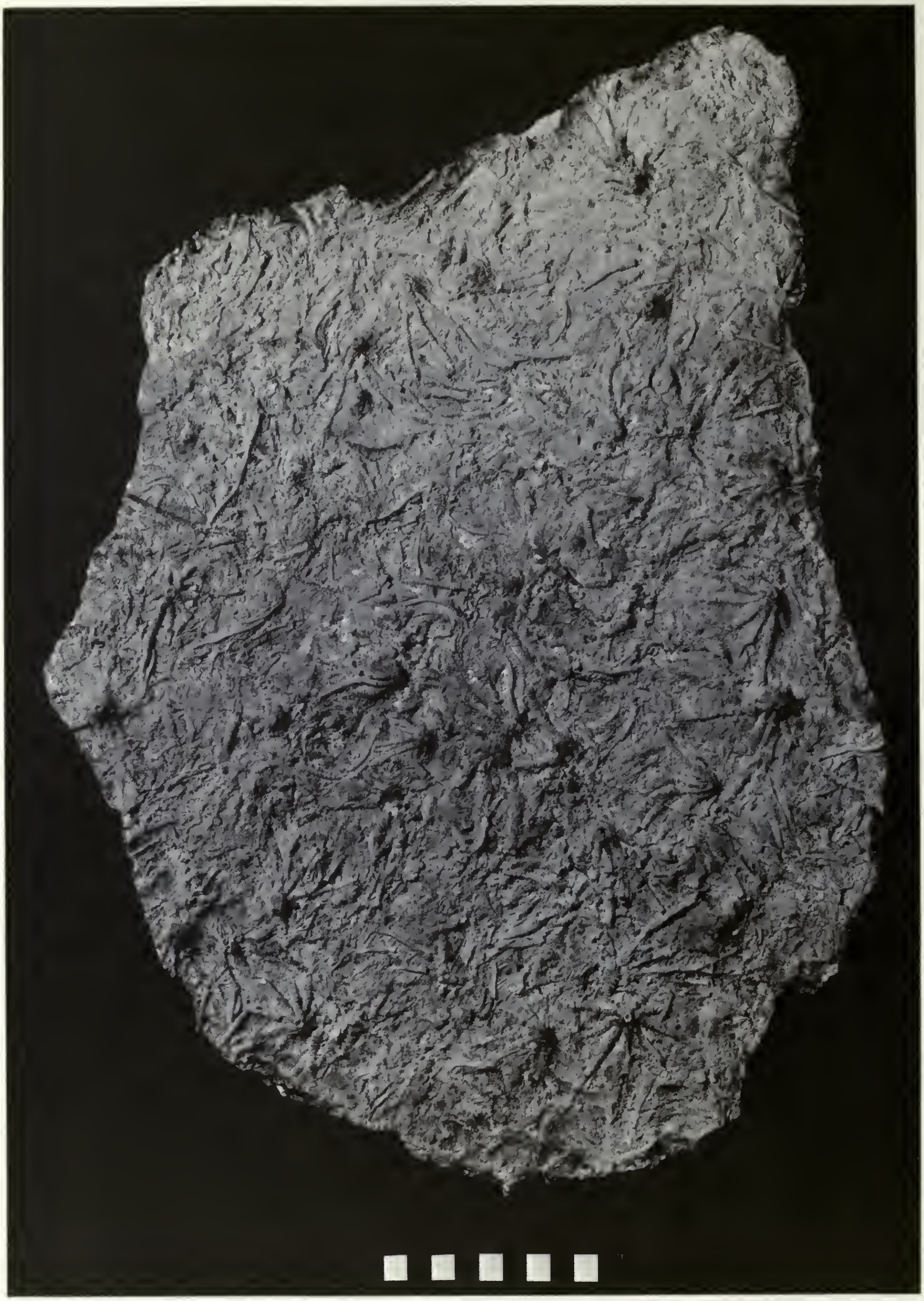


Fig. 2 *Ailsacrinus abbreviatus* gen. et sp. nov. covering a bedding plane from the Eastington crinoid bed (Bathonian, ?Sharps Hill Fm.), BMNH E67791. Most of the crinoids on this undersurface are upright but some are prostrate or obliquely orientated. Divisions of scale bar are 1 cm.

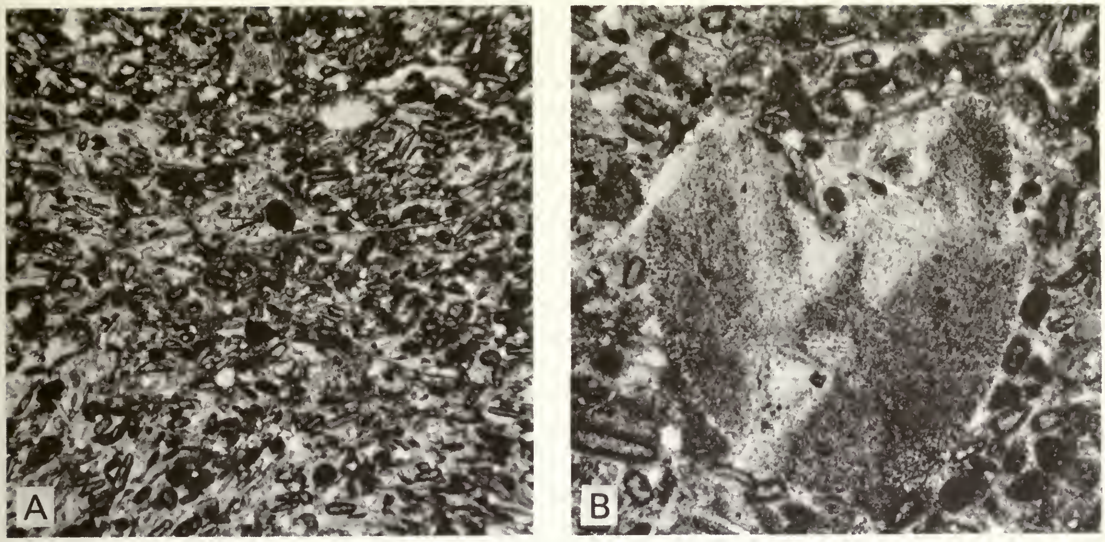


Fig. 3 Thin section cut from the Eastington Crinoid Bed, BMNH E67832. A, sandy bio-oosparite composed mostly of molluscan shell fragments subparallel to bedding; PPL, ×17. B, brachial of *Ailsacrinus abbreviatus* gen. et sp. nov.; PPL, ×33.

contact, by a cross-bedded shelly limestone. Lithologically, the crinoid bed is a grain-supported (grainstone), sandy bio-oosparite composed largely of molluscan shell fragments, 0·1–0·4 mm in length, which are generally orientated parallel to the bedding (Fig. 3). Isolated crinoid ossicles are scarce. Subrounded to subangular quartz grains make up about 20% of the rock and impart a sandy texture to weathered surfaces. Development of the fossils is aided by the presence of thin layers or drapes of clay which are easily washed away from the crinoid-covered bedding planes. The clay contains illite, quartz and calcite (determined by X-ray diffractometry). Good preservation of stereom ultrastructure at this locality is probably the result of clay particles penetrating the outer part of the skeleton and preventing the formation of syntaxial overgrowths within the porous lattice. Apart from the crinoids, macrofossils are sparse and poorly preserved; a few abraded brachiopods, epifaunal bivalves and echinoids are present, together with woody carbonaceous fragments. Preservation of the crinoids is discussed below under Palaeoecology, p. 65.

OTHER LOCALITIES. Richardson (1904: pl. 19, fig. 1) illustrated crowns of *A. abbreviatus* supposedly from the U. Aalenian (*murchisonae* Zone) Lower Limestone of Andoversford, 10 km west of Northleach. These specimens were not from his personal collection and their stratigraphical horizon and provenance may be doubted.

The J. Morris Collection at the BMNH contains a specimen (E67) labelled 'Great Oolite, Corsham, Wiltshire', loc. 6 of Fig. 1.

Carpenter (1882) mentions the occurrence of *M. prattii*, probably referring to *A. abbreviatus*, at Windrush (loc. 4 of Fig. 1), Notgrove (loc. 3) and Miserden Park (loc. 5). Material from Miserden Park includes BMNH E14661 figured in Carpenter's pl. 1, fig. 9. No exact stratigraphical details are given but all may be from low in the Bathonian sequence.

Ailsacrinus prattii

LANSDOWN. The great majority of existing *A. prattii* specimens were obtained over 150 years ago from Lansdown Hill near Bath (loc. 7 of Fig. 1). As early as 1833 Jelly wrote of the small chance of ever procuring further specimens. Lansdown Hill is now part of urban Bath. Initially, Gray (1828) made the mistake of supposing the Lansdown crinoids to have come from the Lias but Jelly corrected this misapprehension and gave their horizon as Great Oolite. A well record from Beckford's Tower at the summit of Lansdown Hill records 30 feet of Great Oolite (Woodward 1894: 243) which, around Bath, is generally regarded as being of late Bathonian *aspidoides* Zone age (Cope *et al.* 1980). The Lansdown crinoids are contained in a matrix of coarse oobiosparite. They are reasonably well articulated but arms are often separated from stem and calyx. Most are preserved in a prostrate attitude, i.e. with the stem lying parallel to bedding. An associated fauna includes well-preserved echinoids. Both Jelly (1833) and Carpenter (1882) mention the occurrence of *Pentacrinites* in association with *A. prattii*. The Sedgwick Museum (Cambridge) collections contain two pieces (J33842, J33850) with isocrinids but these are in a finer-grained rock and are without associated *A. prattii*.

KIRTLINGTON. A single specimen (J14219) in the Oxford University Museum is allegedly from the Great Oolite of Kirtlington (loc. 8 of Fig. 1). This is also likely to be of late Bathonian age and the matrix suggests (T. J. Palmer, personal communication 1979) that it may be from the Lower Cornbrash (*discus* Zone).

Systematic descriptions

Order **MILLERICRINIDA** Sieverts-Doreck *in* Moore *et al.*, 1952
Suborder **MILLERICRININA** Sieverts-Doreck in Moore *et al.*, 1952
Family **MILLERICRINIDAE** Jaekel, 1918
Genus ***AILSACRINUS*** nov.

DIAGNOSIS. Millericrinidae with reduced column, tapering distally and terminated by a rounded columnal; incomplete or lenticular columnals may be present; cup bowl-shaped to conical with small basals and often with irregularly developed, tiny accessory plates, interbasally-placed, generally tuberculate; arms have frequent syzygies; pinnules differentiated into oral and distal series, the oral pinnules having high pinnulars with adoral transverse ridges.

TYPE SPECIES. *Ailsacrinus abbreviatus* sp. nov., Lower–Middle Bathonian (M. Jurassic), Gloucestershire, England. This species is chosen in preference to *A. prattii* because of the superior preservation of available material.

REMARKS. This new genus is proposed to accommodate two aberrant millericrinid species in which the reduced stem with a rounded end is a synapomorphy. They are also distinguished from previously-described millericrinids by having differentiated oral pinnules and abundant syzygies in the arms.

The established species now referred to *Ailsacrinus, Encrinites* (*Apiocrinites*) *prattii* Gray 1828, has usually been placed in the genus *Millericrinus* d'Orbigny, 1841. However, *Millericrinus*, as defined by the type species *Encrinites milleri* von Schlotheim 1823, has a flat-bottomed, five-sided cup with large basals and a stem which does not increase in diameter towards the cup (see Rasmussen *in* Ubaghs *et al*. 1978: fig. 550,1; Roux 1978: fig. 9). *E. prattii* was provisionally included by Rasmussen (*in* Ubaghs *et al*. 1978: T822) in the genus *Liliocrinus* Rollier, 1911, the type species of which was designated by the same authors as *Millericrinus polydactylus* d'Orbigny 1841. In this species the basals and radials are of approximately equal size and the arms divide two or three times, unlike *Ailsacrinus* in which the basals are considerably smaller than the radials and there is only one division of the arms.

NAME. *Ailsacrinus* is named in recognition of Miss Ailsa M. Clark of the Department of Zoology, British Museum (Natural History).

Ailsacrinus abbreviatus sp. nov.

1882 *Millericrinus Prattii* Gray; Carpenter: 29 (*partim*); pl. 1, fig. 9 only.
1904 *Millericrinus Pratti* Gray; Richardson: 250; pl. 19, fig. 1.

DIAGNOSIS. A species of *Ailsacrinus* with small, bowl-shaped cup and tiny triangular basals which either fail to touch or barely touch adjacent basals; radials high relative to basals; accessory plates inconspicuous; column tapering distally and short (1–9 columnals); distal facet of proximale with petaloid areola.

HOLOTYPE. BMNH E67797 (Fig. 25, p. 52), Bathonian (?Sharps Hill Fm.), Eastington, Gloucestershire. P. D. Taylor Coll., 1979.

PARATYPES. BMNH 9570, 9572, 9574, Stonesfield Slate, Northleach; Mantell Coll., 1839. E67, Great Oolite, Corsham, Wiltshire; J. Morris Coll., 1880. E14661 (Carpenter 1882: pl. 1, fig. 9), Forest Marble?, Miserden, Gloucestershire; J. F. Walker Coll., 1908. E14882–5, Lower Great Oolite, Quarry near Isolation Hospital, Northleach; L. Richardson Coll., 1910. E67791–6, E67798–889 and E68070–84, Bathonian (?Sharps Hill Fm.), Eastington, Gloucestershire; P. D. Taylor Coll., 1979.

OCCURRENCE. Lower–Middle Bathonian of Gloucestershire (Fig. 1). The only accurate stratigraphical information available is from Eastington where the rocks exposed are probably of the Sharps Hill Formation, regarded as late early Bathonian (*tenuiplicatus* Zone) or early mid-Bathonian (*progracilis* Zone) in age.

DESCRIPTION. Details of the morphology of *A. abbreviatus* and *A. prattii* are considered together below, p. 45.

REMARKS. This new species has been previously included in *A. prattii* (Carpenter 1882, Richardson 1904). However, these smaller crinoids from the Lower–Middle Bathonian can be distinguished consistently from topotypes of *A. prattii* which occur higher in the Bathonian at Lansdown. The stem of *A. abbreviatus* is less variable and there are none having stems with more than 10 columnals. The cup is smaller and more bowl-shaped than in *A. prattii*, basals are smaller, and accessory plates are less conspicuous, never exceeding one per ray.

NAME. The trivial name *abbreviatus* alludes to the greatly reduced basals and stem in this species.

Ailsacrinus prattii (Gray 1828)

1828 *Encrinites* (*Apiocrinites*) *Prattii* Gray: 219.
1831 *Apiocrinites obconicus* Goldfuss: 187; pl. 57, figs 5a–n.
1833 *A.* [*Apiocrinites*] *fusiformis* Jelly: 46; pl. 1, figs 1–11.
1840 *Millericrinus obconicus* (d'Orb.) [*sic*] d'Orbigny: 80; pl. 14, figs 23–28.
1862 *Apiocrinites obconicus* nobis [*sic*]; Goldfuss: 174; pl. 57, figs 5a–n.
non 1881 *Millericrinus obconicus* d'Orb.–*Apiocrinites obconicus* Goldf.; Morière: 85; pl. 1 (= *Millericrinus morierei* de Loriol 1883).
1882 *Millericrinus Prattii* (Gray) Carpenter: 29 (*partim*); pl. 1, figs 1–8, 10–23 (fig. 9 = *Ailsacrinus abbreviatus* sp. nov.).
1884 *Millericrinus Prattii* (Gray); de Loriol: 618.
1900 *Millericrinus pratti* (Gray); Bather: 135; fig. 52.
1911 *Millericrinus prattii* (Gray); Kirk: 48; pl. 6, figs 1–6.
1934 *Millericrinus prattii* (Gray); Gislén: 6, fig. 7.
1936 *Millericrinus pratti* (Gray); Biese: 464.
1978 *Millericrinus prattii* (Gray); Ubaghs *in* Ubaghs *et al.*: T93; fig. 70,2.
1978 *Liliocrinus prattii* (Gray): Rasmussen *in* Ubaghs *et al.*: T822; fig. 551,2a, b, f, g, i, l.

REVISED DIAGNOSIS. A species of *Ailsacrinus* with moderately large, bowl-shaped to conical cup; basals touching adjacent basals and pentagonal in shape; radials similar in height to basals; accessory plates generally conspicuous, frequently more than one per ray; column tapering distally and of highly variable length (one to more than 66 columnals); distal facet of proximale with tuberculate areola, not petaloid.

HOLOTYPE. The single specimen (Fig. 4) described by Gray (1828), BMNH E24663; Great Oolite (probably Upper Bathonian *aspidoides* Zone), Lansdown, near Bath.

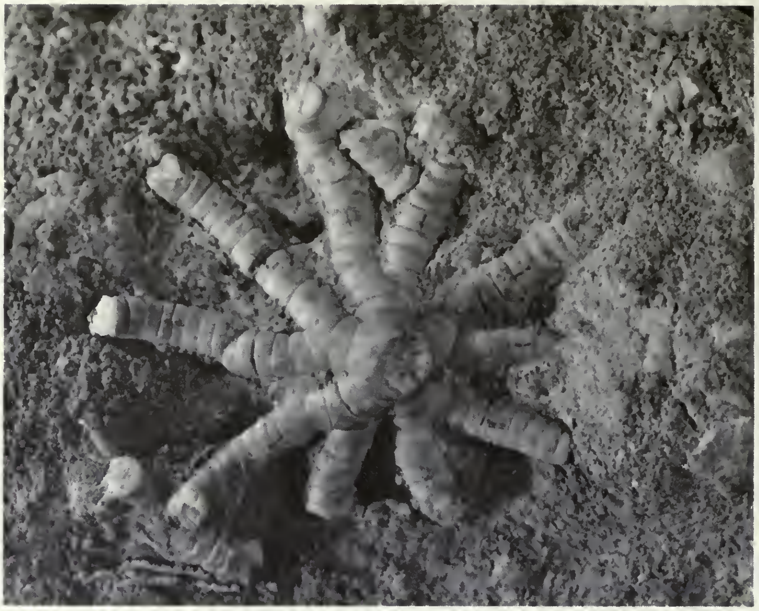


Fig. 4 *Ailsacrinus prattii* (Gray). **Holotype** BMNH E24663, from the Great Oolite of Lansdown Hill; ×2.

Other material. BMNH: 48900, Lansdown; R. Etheridge Coll., 1868. E5722, Great Oolite, Lansdown. E24664, Great Oolite, ?locality; Bowerbank Coll., 1865. OUM: J14219, Great Oolite, Kirtlington. SM: J33689–734, J33769–70, J33806–15, J33822, J33834, Great Oolite, Lansdown; Walton Coll.

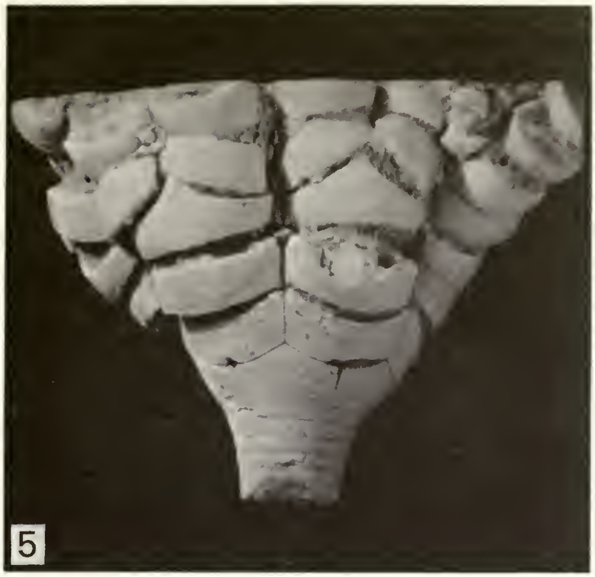
Description. See below.

Remarks. The synonymy lists only those references which give descriptions or figures of *A. prattii*. Elsewhere, the species has been cited as an example of an eleutherozoic crinoid or included in stratigraphical lists of fossils. Pre-1936 references of this type are given by Biese (1936).

Apiocrinites obconicus was described by Goldfuss (1831) using specimens obtained from the Great Oolite of Bath. The illustrations of Goldfuss show that these are clearly conspecific with the earlier *Encrinites prattii* of Gray. D'Orbigny (1840) acknowledged Goldfuss' species but appended his own name as author when referring the species to *Millericrinus*. Crinoids from the Bathonian of Normandy, considered to be the same species by Morière (1881), were later described as *Millericrinus morierei* by de Loriol (1883). They differ from *A. prattii* in having long stems and a more conical, *Apiocrinites*-like transition between stem and cup.

Jelly (1833) was aware that the Lansdown species had been named *Encrinites prattii* by Gray (1828) but, being critical of Gray because he had stated incorrectly that their horizon was Lias and also employed a specific name derived from a proper name, chose to ignore this name. Instead, he called the crinoid the 'Lansdown Encrinite' throughout most of his paper before, in a concluding paragraph (p. 46) stating ' . . . this, perhaps, might not incorrectly be called *A.* [*Apiocrinites*] *fusiformis*'.

Knowledge of *Ailsacrinus prattii* (Gray) derives largely from the description and figures of Carpenter (1882). Although these are based mostly on Lansdown material, one of Carpenter's figures (pl. 1, fig. 9) is a specimen (BMNH E14661) from Miserden and is here considered to be *A. abbreviatus* sp. nov. Bather (1900), Kirk (1911), Gislén (1934) and Ubaghs *et al.* (1978) all copied, directly or indirectly, Carpenter's figures.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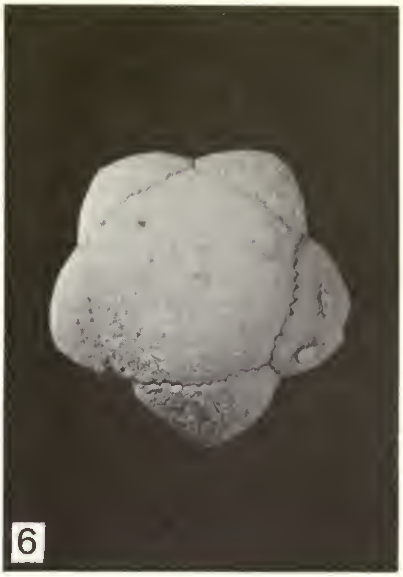
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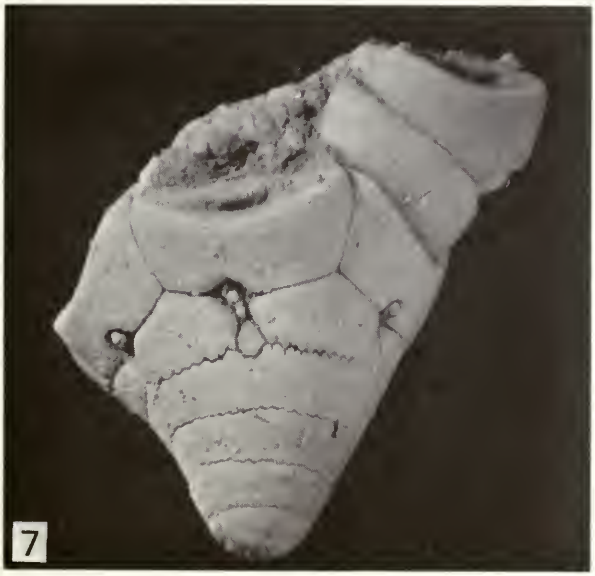
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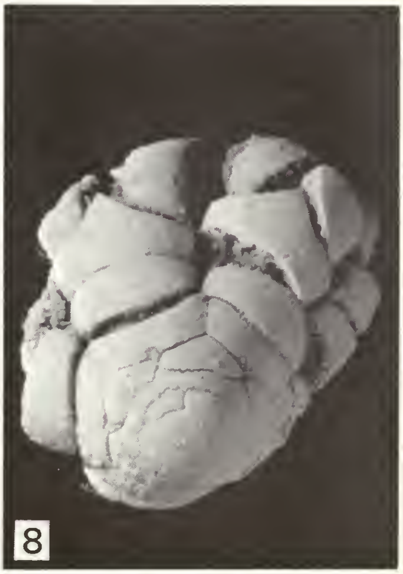
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Figs 5–8 *Ailsacrinus prattii* (Gray), Great Oolite, Lansdown Hill. Specimens coated with ammonium chloride. Fig. 5, BMNH E5722, crown and proximal columnals of a presumed long-stemmed individual; ×3·5. Fig. 6, SM J33704, crinoid with a stem composed of a single rounded columnal attached to the basals; ×7. Fig. 7, SM J33700, crinoid with a short conical stem and several accessory plates in the cup; ×6. Fig. 8, SM J33719, short-stemmed crinoid with irregular lenticular columnals; ×4.

Morphology

Stem

The feature of *Ailsacrinus* which has attracted most attention is the short, variable stem tapering distally towards a rounded terminal columnal.

Carpenter (1882) emphasized the extreme variability in length of the stem among individuals of *A. prattii* from Lansdown. The longest-stemmed Lansdown crinoid has an incomplete stem of

66 columnals totalling more than 50 mm in length (Carpenter 1882: pl. 1, fig. 14). In contrast, the incomplete stem of another crinoid (pl. 1, fig. 6), although only 27 mm long, possesses 58 columnals. At the other extreme is an individual (SM J33704; pl. 1, fig. 18) with a stem composed of a single, gently convex columnal (Fig. 6). Were it not for the lack of cirri this plate would be virtually indistinguishable from a comatulid centrodorsal. Three other specimens (SM J33709, J33712 and J33715) also appear to have stems of one columnal only although these are higher than that of J33704. Two individuals have stems of two columnals only and ten others have numbers between 4 and 53; see caption to Fig. 9.

The mean value of stem length in these crinoids is equivalent to 12·5 columnals, though this figure may be an underestimate of the true population mean because the stems of crinoids with short stems are more likely to be preserved unbroken. The distribution is very strongly positively skewed with a mode of 1 columnal per stem.

The stem of *A. abbreviatus* is generally shorter than *A. prattii* and there is less variability. Fig. 9 shows the frequency of stems of different length. Again, the mean value of 4·2 columnals may be an underestimate of the true mean for the same reasons as for *A. prattii*. The longest stems consist of 9 columnals, the shortest 1 columnal (Fig. 11), and the modal value for the sample is 2 columnals. The longest stems are about 11 mm long, whereas 3 mm is a typical length.

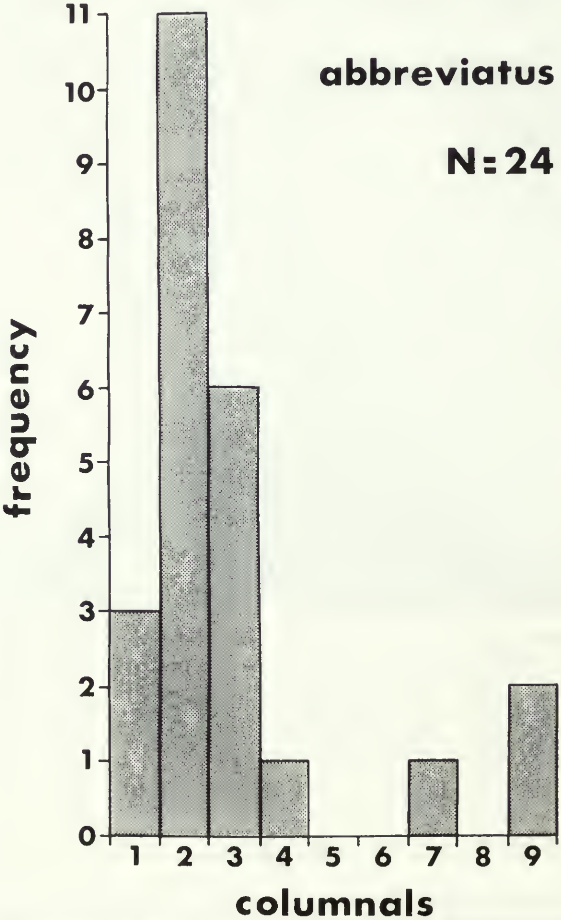


Fig. 9 Size frequency histogram of stem length (expressed as number of columnals) in 24 individuals of *Ailsacrinus abbreviatus* gen. et sp. nov. from Eastington. In contrast, 16 individuals of *A. prattii* (Gray) from Lansdown Hill showed the following numbers of columnals: 1 (4 individuals); 2 (2 individuals); 4, 5, 6, 7, 14, 17, 21, 32, 33, 53 (1 individual each).

Proximal columnals in *Ailsacrinus* have a greater diameter than distal ones, the stem tapering away from the cup. The angle of taper tends to be greater in stems with fewer columnals, for example compare Figs 7 and 20A. The proximal–distal gradient of decreasing columnal width is quantified for two long-stemmed individuals of *A. prattii* in Fig. 43 (p. 62) and is discussed below under Ontogeny (p. 58).

The most distal columnal in the majority of *Ailsacrinus* specimens has a smooth rounded end (Figs 6, 8, 11). In some cases the axial lumen is exposed but in others it appears to be plugged, as in some isocrinids (Ubaghs *et al.* 1978: T848). Certain specimens of *A. abbreviatus* have a distal columnal which, rather than being rounded, exhibits a corroded petaloid crenularium of a symplectial articulation facet (Figs 13, 14). Though observed in somewhat weathered material, this may well have been the condition of the columnal in the living crinoid prior to burial. No individuals are known with massive encrusting holdfasts, so typical of millericrinids, or the cirri which typify many other articulates. A small branching structure resembling a stem with some columnal fusion occurs on a slab (SM J33693) with arms of *A. prattii* and is depicted by Carpenter (1882: pl. 1, fig. 5). This was interpreted by both Jelly (1833) and Carpenter (1882) as a possible 'root' but unfortunately is incompletely preserved and a teratological origin cannot be discounted.

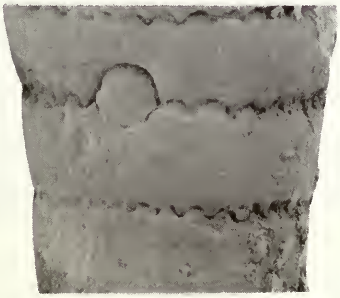
The stem of *Ailsacrinus* is homomorphic; nodals are not detectable on the basis of columnal size. Long-stemmed individuals of *A. prattii* do, however, exhibit a proximal–distal gradient of changing columnal height. Usually columnals decrease in height away from the cup but in one specimen (SM J33694) the reverse holds true (Fig. 42, p. 61).

Incomplete or 'lenticular' (Carpenter 1882) columnals are fairly common in both *A. prattii* and *A. abbreviatus*. These fail to encompass the entire circumference of the stem (Figs 8, 10, 20A). When traced around the stem they 'pinch-out' or boudinage and the space they would have occupied is taken up by thickening of the two contiguous columnals.

A single specimen of *A. prattii* (SM J33707) has an unusual overgrowth extending downwards from the cup to cover the top of the stem (Carpenter 1882: pl. 1, fig. 21). This irregular structure consists of two columnal-like plates, one of which is incomplete.

Poorly-preserved stereom on the outer surface of *A. abbreviatus* columnals appears labyrinthic in form with a spacing of 5–10 μm between elements of the lattice.

Articulations between columnals are symplectial. Externally, the crenellae and culmina are seen to interlock in a crenulate manner (Fig. 10). The distal facet of the top columnal in *A. abbreviatus* has a petaloid areola and a quinquelobate lumen (Fig. 14). In *A. prattii* the crenularium has crenellae and culmina which are better defined, and the areola is not petaloid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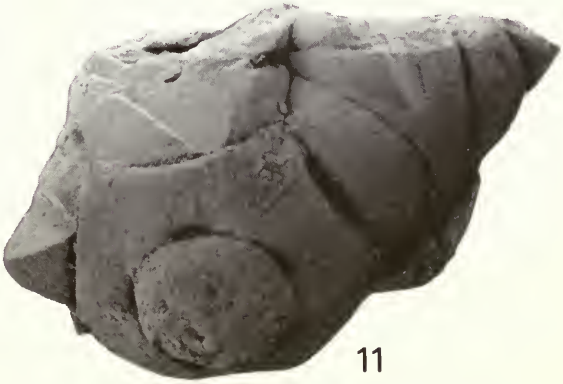
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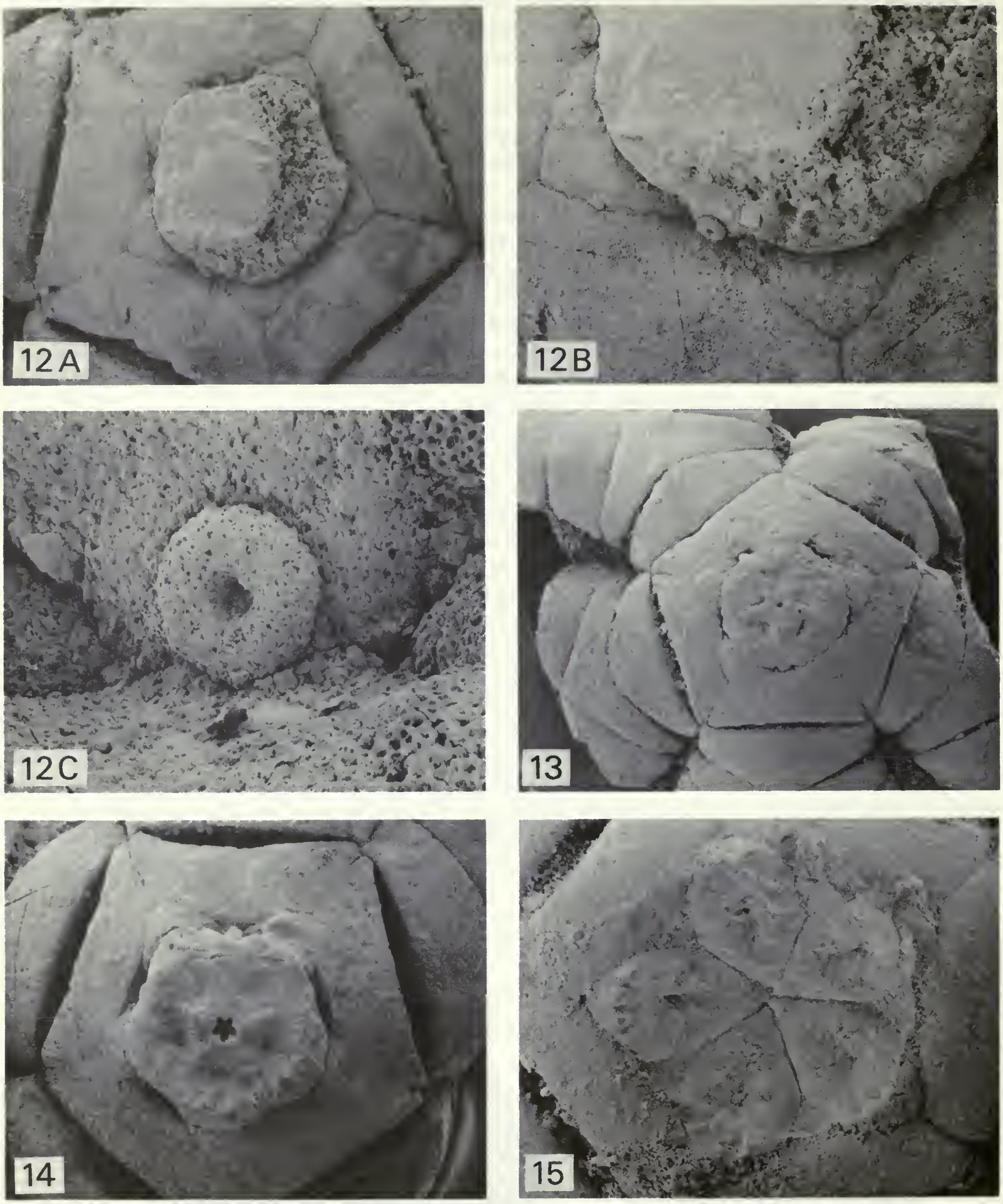
Figs 10–11 Scanning electron micrographs of the stem in *Ailsacrinus abbreviatus* gen. et sp. nov., Bathonian (? Sharps Hill Fm.), Eastington. Fig. 10, BMNH E68070, part of a long stem showing crenulate symplectial articulations and a small lenticular columnal; × 11. Fig. 11, BMNH E68071, short stem composed of a rounded columnal corroded in appearance; × 5·5.



Figs 12–15 Scanning electron micrographs of the cup in *Ailsacrinus abbreviatus* gen. et sp. nov., Bathonian (? Sharps Hill Fm.), Eastington. Fig. 12, BMNH E68072: A, aboral view showing broken stem, small basals and radials; ×3·7; B, tuberculate accessory plate located between basals; ×15·7; C, detail of tubercle; ×83. Fig. 13, BMNH E68073, cup with a solitary columnal attached; ×4·9. Fig. 14, BMNH E68074, corroded petaloid crenularium and axial lumen of top stem columnal; ×7. Fig. 15, BMNH E68075, stemless specimen showing basal facets; ×9·1.

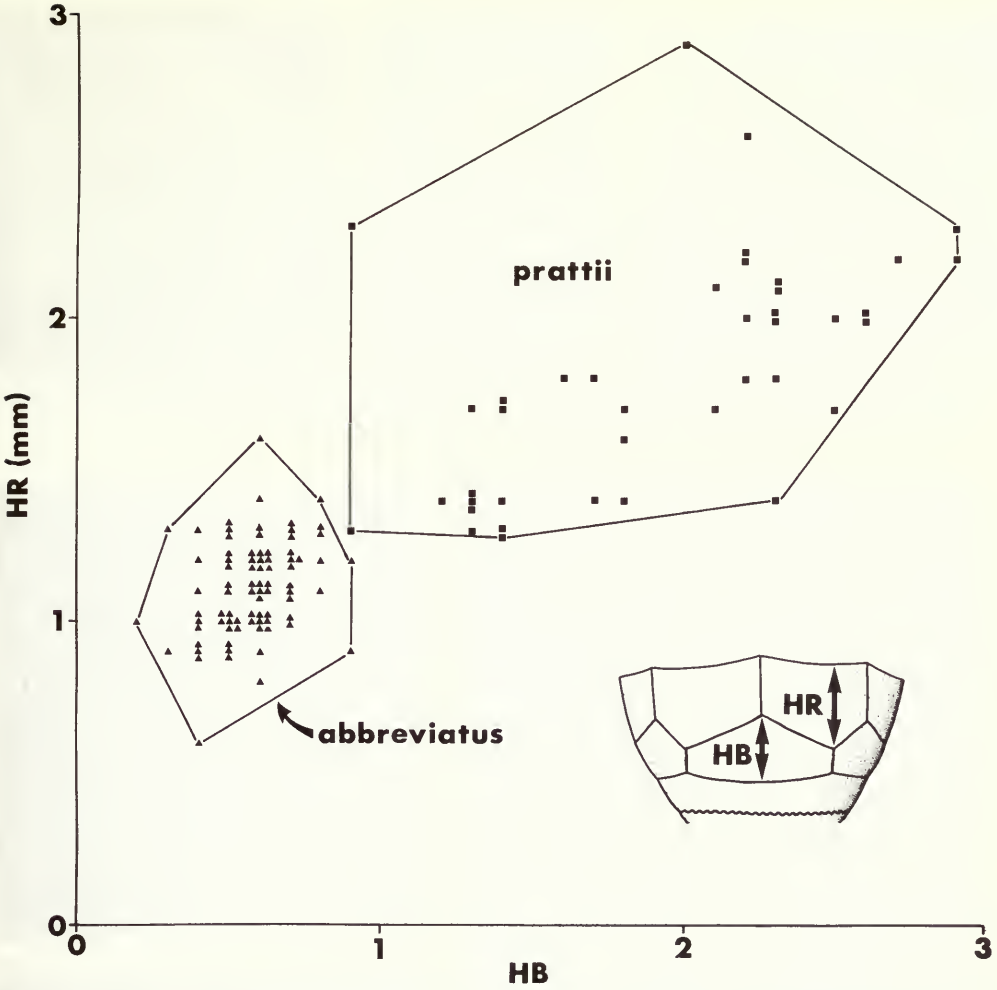


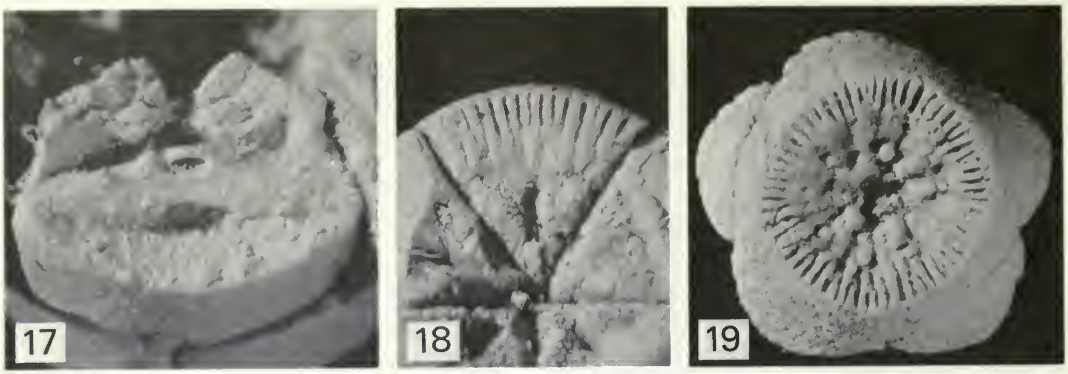
Fig. 16 Height of basals plotted against height of radials in *Ailsacrinus abbreviatus* gen. et sp. nov. and *A. prattii* (Gray).

but has radiating rows of tubercles (Fig. 19). The proximal facet of the top columnal, articulating with the basals, is a weakly marked symplexy or cryptosymplexy in *A. abbreviatus* but more strongly marked in *A. prattii*. The high pyramidal form of this facet suggests permanent attachment of the columnal to the cup, i.e. that the topmost columnal is a proximale. However, the columnal is not united to the cup by a synostosis as in the Recent crinoids discussed by Breimer *in* Ubaghs *et al.* (1978: T25).

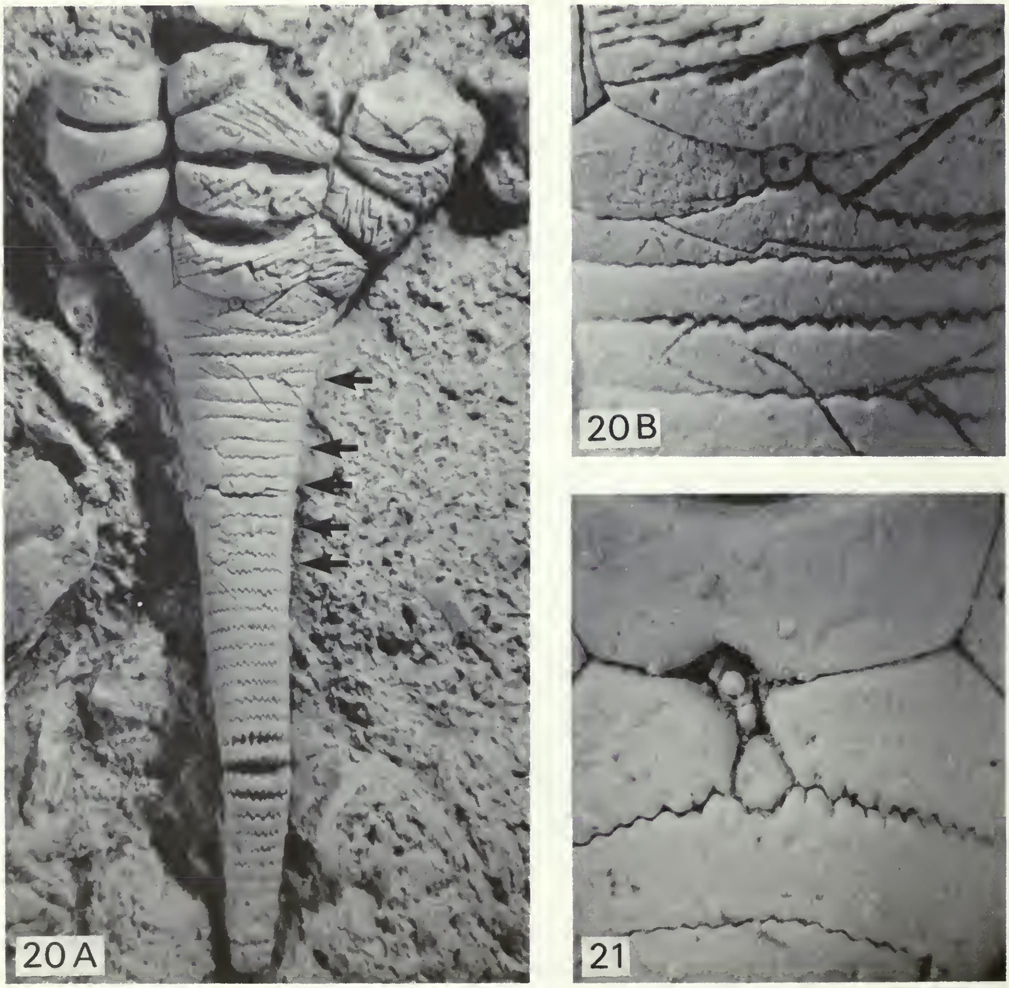
Dorsal cup

The cup is small and bowl-shaped (Ubaghs *in* Ubaghs *et al.* 1978: fig. 72) in *A. abbreviatus* (Fig. 46, p. 66), rather larger and more conical in *A. prattii* (Fig. 5). A depressed base (Fig. 15) accommodates the pyramidal facet of the top columnal. Syntaxial overgrowths obscure details of the adoral interior of the cup in all specimens examined. However, external preservation of plates is good.

Basals are very small and triangular in *A. abbreviatus*. Externally, adjacent basals either fail to touch or barely touch one another (Figs 12–14). They are seen, however, to make contact internally in specimens whose stems have been removed (Fig. 15). Basals of *A. prattii*, though



Figs 17–19 *Ailsacrinus prattii* (Gray), Great Oolite, Lansdown Hill. Specimens coated with ammonium chloride. Fig. 17, SM J33707, radial facet; × 11. Fig. 18, SM J33703, basal facet; × 8. Fig. 19, SM J33708, distal facet of top columnal; × 7.

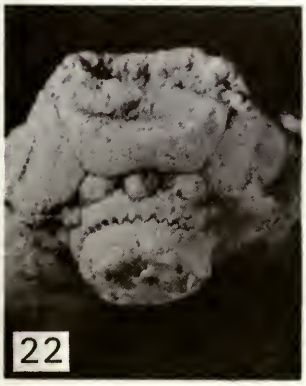


Figs 20–21 *Ailsacrinus pratti* (Gray), Great Oolite, Lansdown Hill. Specimens coated with ammonium chloride. Fig. 20, SM J33695: A, long stem with 5 lenticular columnals (arrowed); × 3·9; B, proximal columnals and tuberculate accessory plate; × 12. Fig. 21, SM J33700, ray containing several irregular accessory plates, one of which is tuberculate; × 12.

also reduced in size, are larger and touch adjacent basals externally giving them a five-sided external shape (Figs 5–8). The proximal facet of each basal has a median radial depression and a marginal crenularium which, like the facet of the adjoining columnal, is well-developed in *A. prattii* (Fig. 18) but poorly-developed in *A. abbreviatus* (Fig. 15). The facet between basals and radials has not been observed.

Radials exceed the height of basals in *A. abbreviatus* but are of about the same height in *A. prattii* (Fig. 16). Their distal articulating facet (i.e. that which articulates with the first brachials) is inclined at a variable angle to the long axis (proximal–distal) of the crinoid. An angle of 15° has been estimated in *A. abbreviatus* and angles between 30° and 60° in *A. prattii*. This variability may relate, at least in part, to the attitude of burial and the nature of plate disarticulation during compaction. Radial facets have a deep aboral ligamental fossa, small interarticular ligamental fossae and large muscular fossae (Fig. 17).

In addition to the usual plates of the cup, small accessory plates are a characteristic feature of *Ailsacrinus*. These seem to be present in a minority of individuals of *A. abbreviatus* where they are generally inconspicuous, but are present in most specimens of *A. prattii*. Those individuals of *A. abbreviatus* with accessory plates do not usually have them in every ray. Accessory plates are more numerous in *A. prattii*, some individuals having up to 3 or 4 plates per ray (Fig. 21). Their position is perradial, i.e. between basals. Sometimes the accessory plates are in contact with the top stem columnal (Figs 20B, 22), particularly in *A. abbreviatus* where the basals are small and not contiguous. In *A. prattii* accessory plates are often located at a triple junction between two basals and a radial (e.g. right-hand accessory plate of Carpenter 1882: pl. 1, fig. 3), or they may be extended distally into embayments within radials (Fig. 21). Large accessory plates in some *A. prattii* specimens are located in the basal circlet in contact with both column and radials (e.g. left-hand accessory plate of Carpenter 1882: pl. 1, fig. 3). Several specimens of *A. prattii* have shallow pits in the cup which are in appropriate locations to have accommodated large accessory plates (Fig. 5). Most are vacant but some are occupied by small accessory plates. An interesting feature of the accessory plates is the presence of tubercles on some of them. These resemble the spine-bearing tubercles of echinoids in having a mamelon and a central foramen (Fig. 12C). The sporadic occurrence of accessory plates led Carpenter (1882: 35) to suppose that they were 'without any morphological importance'. However, they seem to be present in too many individuals for Carpenter's opinion to be acceptable. Among living crinoids they would appear to have no close analogues. Andrew Smith (personal communication 1981) has suggested a comparison with statocysts, balancing structures developed in several groups of echinoderms. Kirk (1911) identified accessory plates as infrabasals. Some specimens of *A.*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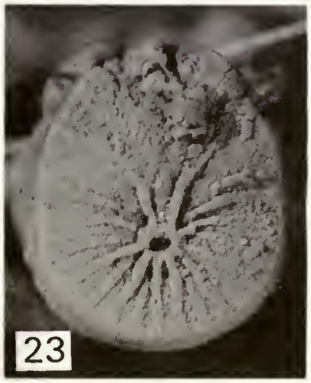
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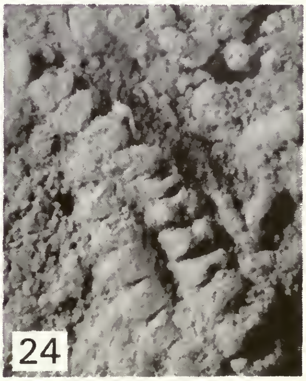
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Figs 22–24 *Ailsacrinus abbreviatus* gen. et sp. nov., Bathonian (? Sharps Hill Fm.), Eastington. Specimens coated with ammonium chloride. Fig. 22, BMNH E68076, unusually large accessory plate and poorly-preserved radial facet; × 17. Fig. 23, BMNH E68077, facet of the most proximal syzygy (on the distal side of secundibrach 4) showing numerous culminae; × 18. Fig. 24, BMNH E68078, oral pinnules lying across the adoral surface of the calyx; × 12.

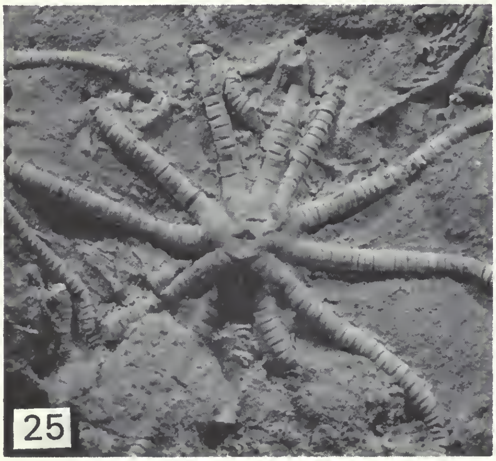
abbreviatus have tabular plates concealed between the basals which resemble the infrabasals of *Liliocrinus polydactylus* (d'Orbigny) illustrated by Ubaghs *in* Ubaghs *et al.* (1978: fig. 73,5). However, their relationship with accessory plates is unclear.

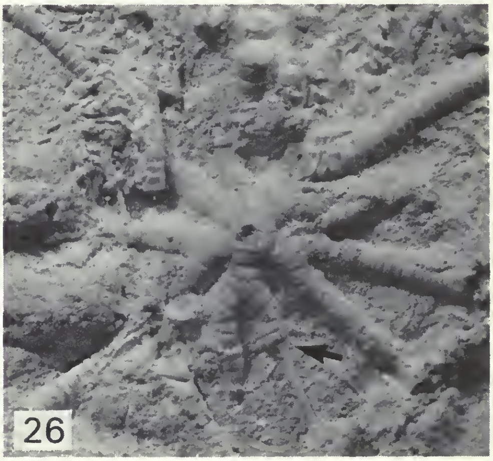
Tegmen

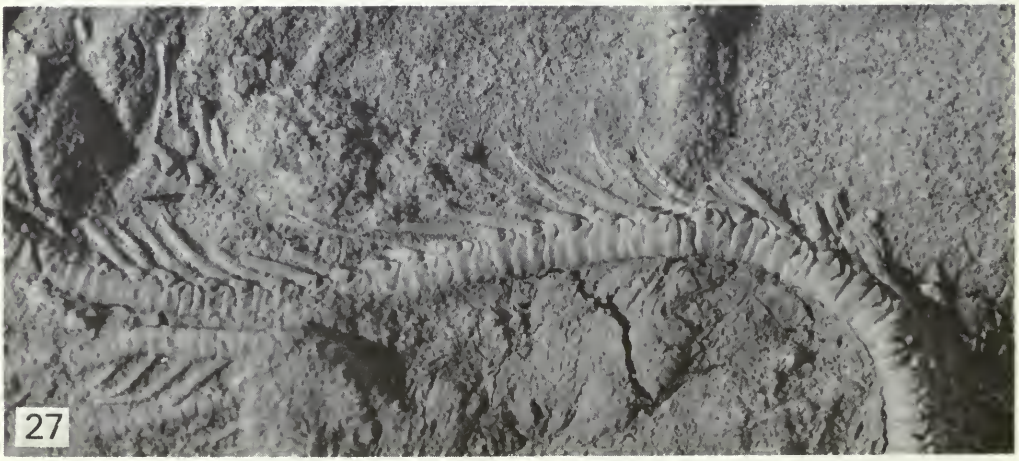
Definite tegminal plates have not been identified in *Ailsacrinus*, although a mass of small plates originally above the displaced calyx in a specimen of *A. prattii* (SM J33712) may include tegminal plates as well as pinnulars. Alternatively, the tegmen in *Ailsacrinus* may have been like that of many living comatulids, i.e. naked with the exception of microscopic skeletal elements.

Arms

Arm morphology was discussed little by Carpenter (1882), whose material consisted mostly of Lansdown crinoids lacking arms or with disarticulated brachials. In contrast, the specimens of *A. abbreviatus* from Northleach often display finely-preserved arms (Figs 25–27). In several







Figs 25–27 *Ailsacrinus abbreviatus* gen. et sp. nov., Bathonian (? Sharps Hill Fm.), Eastington. Fig. 25, **Holotype** BMNH E67797, cup and radially-arranged arms (eleven-armed appearance is due to the presence of an arm from a second individual); ×1. Fig. 26, BMNH E67808, crinoid with regenerated arm arising from the most proximal syzygy (arrowed); ×1·6. Fig. 27, BMNH E67794, pinnulated arm resting on a bedding plane; ×2·1.

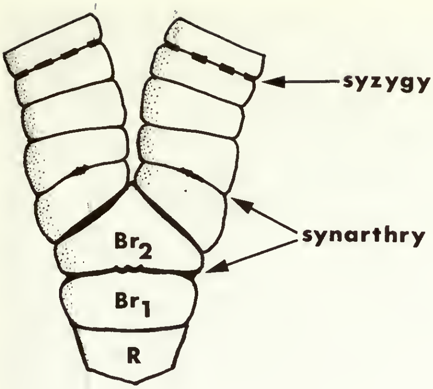


Fig. 28 Diagram showing proximal brachial articulations in *Ailsacrinus* gen. nov. With the exception of the synarthries and the syzygy all articulations are muscular. R, radial; Br_1, 1st primibrach; Br_2, 2nd primibrach.

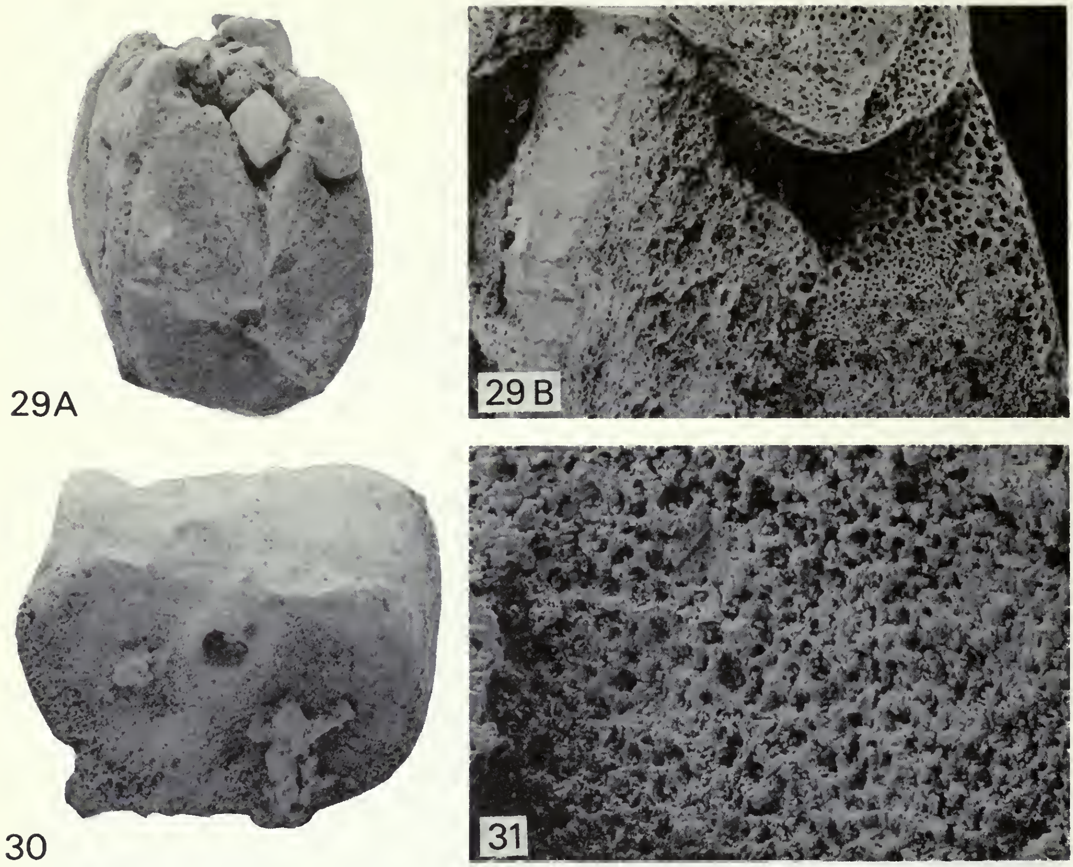
individuals these seem to be almost completely preserved, interrupted only by minor disarticulation and dislocation. However, the tendency for arms to be preserved lying oblique to bedding means that their entire length is never seen. There would appear to be no significant difference in arm structure between *A. abbreviatus* and *A. prattii*. Both have identical patterns of articulation and similarly-shaped brachials, though rather larger in *A. prattii*. The arms divide only once and hence *Ailsacrinus* is ten-armed. Arms in *A. abbreviatus* have been observed to exceed 19 cm in length.

The first primibrach has a muscular articulation with the radial, and the second primibrach is an axillary (Fig. 28). Therefore the first brachitaxis contains two brachials, a common condition in articulate crinoids. However, an *A. prattii* specimen (SM J33709) illustrated by Carpenter (1882: pl. 1, fig. 23) has two rays containing a third primibrach. A single ray of an *A. abbreviatus* individual (BMNH E68072) contains only one primibrach, the axillary, in the first brachitaxis. These rare variants may be meristic or perhaps pathological.

Articulations between primibrachs 1 and 2, and between secundibrachs 1 and 2, are synarthrial (Fig. 28). Synarthrial facets have depressed ligamental fossae on either side of a fulcral ridge with an adoral–aboral orientation (Fig. 30). Stereom of the ligamental fossae does not show well-defined galleries in specimens examined by electron microscope (Fig. 31).

A second kind of nonmuscular articulation occurring commonly in the arms of *Ailsacrinus* is a syzygy. The first syzygy (Fig. 28) is situated between secundibrachs 4 and 5 (unlike in comatulids, where it generally occurs between secundibrachs 3 and 4; Rasmussen *in* Ubaghs *et al.* 1978) and subsequent syzygies are present at frequent intervals along the arm. On average, about 25% of joints are syzygial, and the intersyzygial interval is 2, 3 or 4 muscular joints. Some, but not all, lengths of arm of *A. abbreviatus* display a regular pattern (Fig. 32) of syzygies separated alternately by 2 and 4 muscular joints.

Syzygial facets have a series of culmina radiating from the axial canal (Figs 23, 33, 34A, B). The number of culmina per facet is variable, ranging from about 7 (Fig. 34A) to 20 (Fig. 23). Occasionally, the culmina are reduced to a row of tubercles, in the manner of isocrinid cryptosyzygies (Breimer *in* Ubaghs *et al.* 1978: T38). Culmina of adjoining brachials are clearly seen to oppose (Figs 35A, B). Stereom of the culmina is dense and consists of closely-spaced broad rods, 15–20 μm in width, linked by small cross-struts (Fig. 34C); orientation of the rods is approximately concentric about the axial lumen. This results in some of the rods being oblique to the culmina on which they are situated. Culmina stereom appears to have been strong and capable of resisting abrasion caused by adjacent brachials rubbing against one another. Though similarly dense, stereom of the culmina in the living comatulid *Nemaster rubiginosa* (Macurda, Meyer & Roux *in* Ubaghs *et al.* 1978: fig. 191,4) contrasts with that of *Ailsacrinus* in having a knobbly appearance without a directional fabric. Stereom of the crenellae, which is presumed to have served as an anchorage for ligament, in *Ailsacrinus* appears to be galleried with a pore diameter of about 5 μm (Fig. 34C).



Figs 29–31 Scanning electron micrographs of muscular and synarthrial articulations in *Ailsacrinus abbreviatus* gen. et sp. nov., Bathonian (? Sharps Hill Fm.), Eastington. Fig. 29, BMNH E68079: A, poorly-preserved, moderately oblique muscular facet; × 10·8; B, fine stereom of the muscular fossa; × 67. Figs 30–31, BMNH E68074: Fig. 30, synarthrial facet; × 25; Fig. 31, stereom of the ligamentary fossa of a second synarthrial facet; × 185.

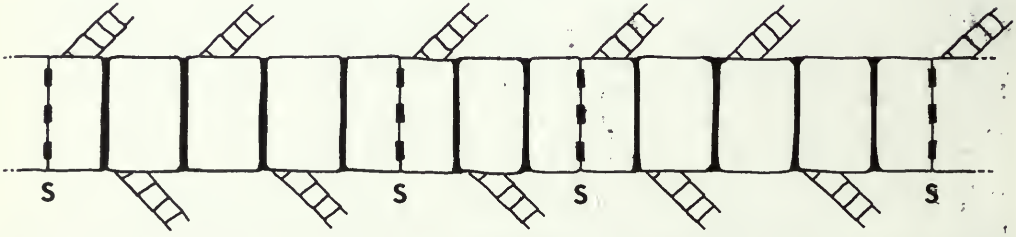
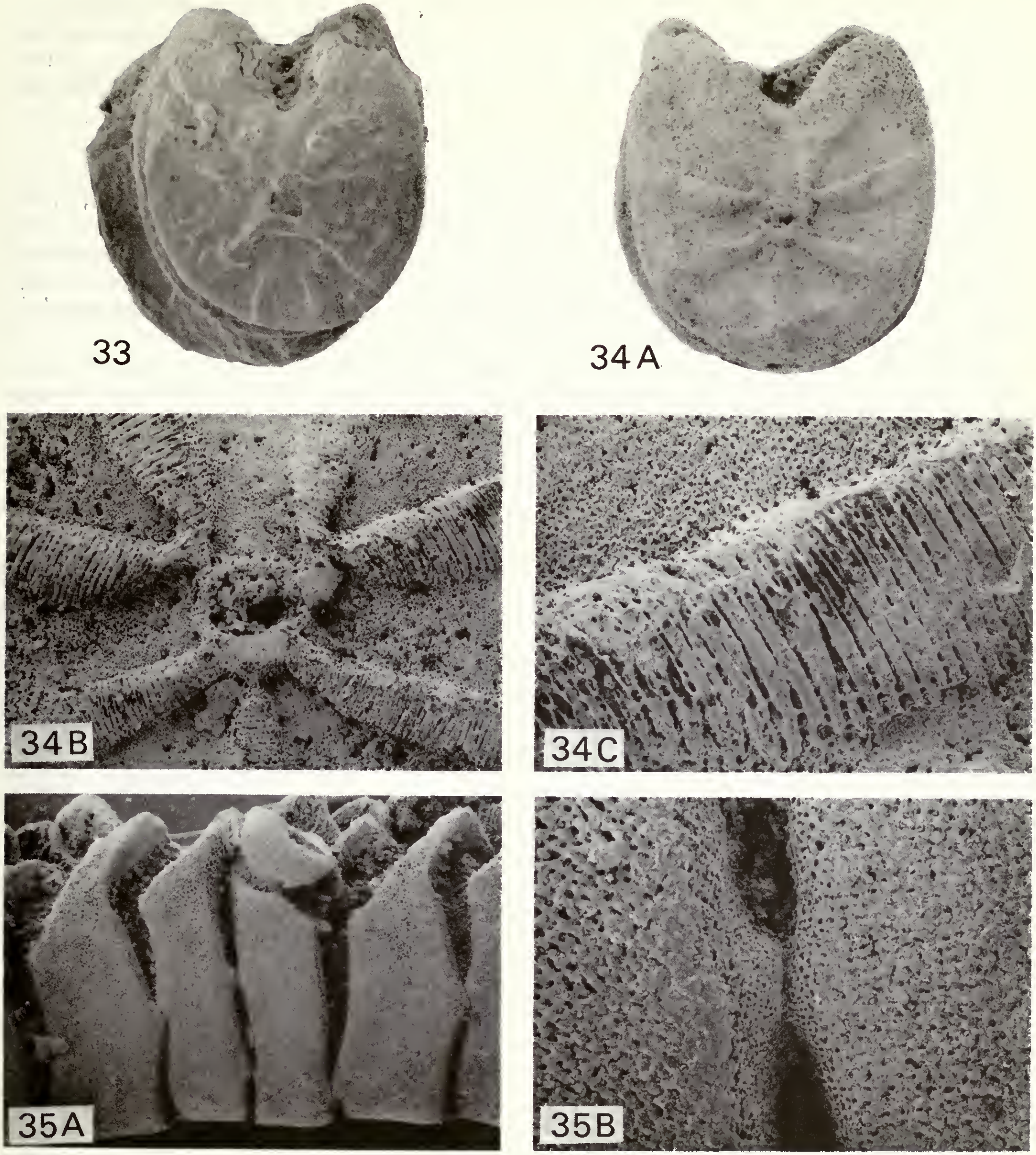


Fig. 32 Diagram showing a common pattern of distribution of brachial articulations and pinnules in the arms (viewed aborally) of *Ailsacrinus abbreviatus* gen. et sp. nov. Syzygies are beaded and labelled 'S'; the remaining articulations are muscular.

Brachials situated proximally and distally of a syzygy, hypozygals and epizygals respectively, are rather narrower than other brachials (Fig. 35A). When arm regeneration is observed, the regenerated arm always arises from a syzygial joint, in one instance from the most proximal syzygy in the arm (Fig. 26). Regeneration from a syzygy was illustrated by Jelly (1833: figs 4, 5) and is a characteristic of most living crinoids (Breimer *in* Ubaghs *et al.* 1978: T34).



Figs 33–35 Scanning electron micrographs of syzygial articulations in *Ailsacrinus* gen. nov. Fig. 33, *A. prattii* (Gray), BMNH E5722 (fragment), Great Oolite, Lansdown Hill; syzygial facet with poorly-developed culminae; × 15. Fig. 34, *A. abbreviatus* sp. nov., BMNH E68080, Bathonian (? Sharps Hill Fm.), Eastington: A, syzygial facet with well-developed culminae; × 18·5; B, culminae radiating from the axial canal; × 52; C, stereom of culmina and crenellae; × 130. Fig. 35, *A. abbreviatus* sp. nov., BMNH E68081, Bathonian (? Sharps Hill Fm.), Eastington: A, lateral view of an arm showing narrow hypozygal and epizygal brachials; × 10·4; B, opposing culminae of hypozygal and epizygal; × 56.

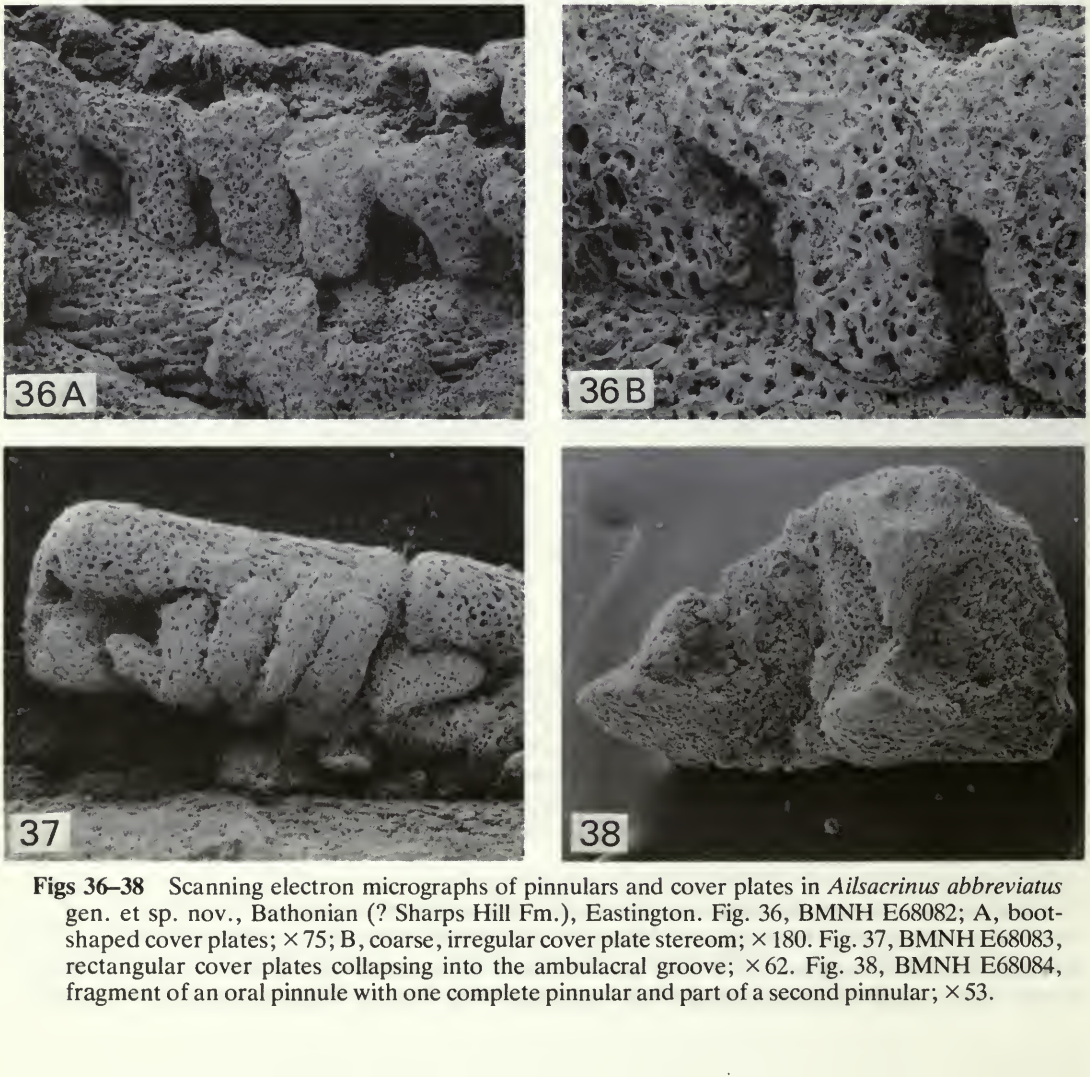
Muscular facets are rarely observed in *A. abbreviatus* because pre-fossilization arm breakage invariably occurred at syzygies and articulated brachials are now firmly bound together with syntaxial calcite overgrowths. Unfortunately stereom preservation is poor in Lansdown *A. prattii* where muscular articulation facets are more commonly visible. Muscular articulations in

Ailsacrinus are slightly to moderately oblique. Facets show a large aboral ligamental fossa and have an adoral region above the fulcral ridge where a poorly-defined break in slope appears to separate large interarticular ligamental fossae from small muscular fossae (Fig. 29A). A layer of fine stereom apparently overlies coarser stereom in the muscular fossa of a poorly-preserved specimen of *A. abbreviatus* (Fig. 29B).

Pinnules

Pinnulation in *Ailsacrinus* is relatively complete. The two primibrachs and secundibrach 1 lack pinnules, and so the first pinnule arises from secundibrach 2. Thereafter pinnules arise on alternate sides of the arm from each brachial, with the exception of hypozygals preceding syzygies. The distribution of syzygies means that along each side of the arm, pinnules are borne on either every second or on every third brachial (Fig. 32). There are at least two distinct types of pinnules in *Ailsacrinus*, an oral series and a distal series.

Oral pinnules occur in the proximal parts of the arms and are generally found lying across the adoral surface of the calyx (Fig. 24). There seem to be two or three pairs of oral pinnules on each arm. Although complete oral pinnules have not been seen, their preserved length and taper suggests that they are shorter than distal pinnules. Oral pinnules lack ambulacral grooves and associated cover plates, and their pinnulars are short and high. Each pinnular has an adoral



Figs 36–38 Scanning electron micrographs of pinnulars and cover plates in *Ailsacrinus abbreviatus* gen. et sp. nov., Bathonian (? Sharps Hill Fm.), Eastington. Fig. 36, BMNH E68082; A, boot-shaped cover plates; × 75; B, coarse, irregular cover plate stereom; × 180. Fig. 37, BMNH E68083, rectangular cover plates collapsing into the ambulacral groove; × 62. Fig. 38, BMNH E68084, fragment of an oral pinnule with one complete pinnular and part of a second pinnular; × 53.

median transverse ridge (Fig. 38), broad at the two outer edges of the pinnular and narrow at the centre. Coarse stereom flanks the ridge. In profile, this ridge forms a triangular-shaped top to the pinnular. The nature of articulations between oral pinnulars is unknown. The function of oral pinnules in living crinoids is unclear but they may have roles in defence, manipulation of food particles, and/or fixation.

Distal pinnules have ambulacral grooves and are composed of comparatively elongate pinnulars (Fig. 39A). The maximum observed length of a distal pinnule in *A. abbreviatus* is over 2 cm in an incomplete pinnule composed of 28 pinnulars. However, another distal pinnule in the same species was complete and consisted of 21 pinnulars. Distal pinnules are terminated by a pinnular which tapers to a point. The articulation between brachials and pinnular 1 is muscular with a fulcral ridge orientated almost parallel to the length of the arm. The articulation between pinnulars 1 and 2 is also muscular but the articulation between pinnulars 2 and 3 is synarthrial. The presence of a large aboral ligament is responsible for the gap commonly observed between the short pinnular 1 and pinnular 2, when viewed from the side (Fig. 39B). Stereom on the outer sides of distal pinnulars is fascicular (Fig. 39C), rather like that of syzygial culmina but contrasting with stereom of the brachials (Fig. 39D). Broad rods (15–20 μm in width) connected by cross-struts parallel the length of the pinnular and are orientated slightly obliquely to the surface of the pinnular. The rods have distally directed pointed ends (Fig. 39C). Minute rectangular or boot-shaped cover plates border the ambulacral groove (Figs 36A, B, 37).

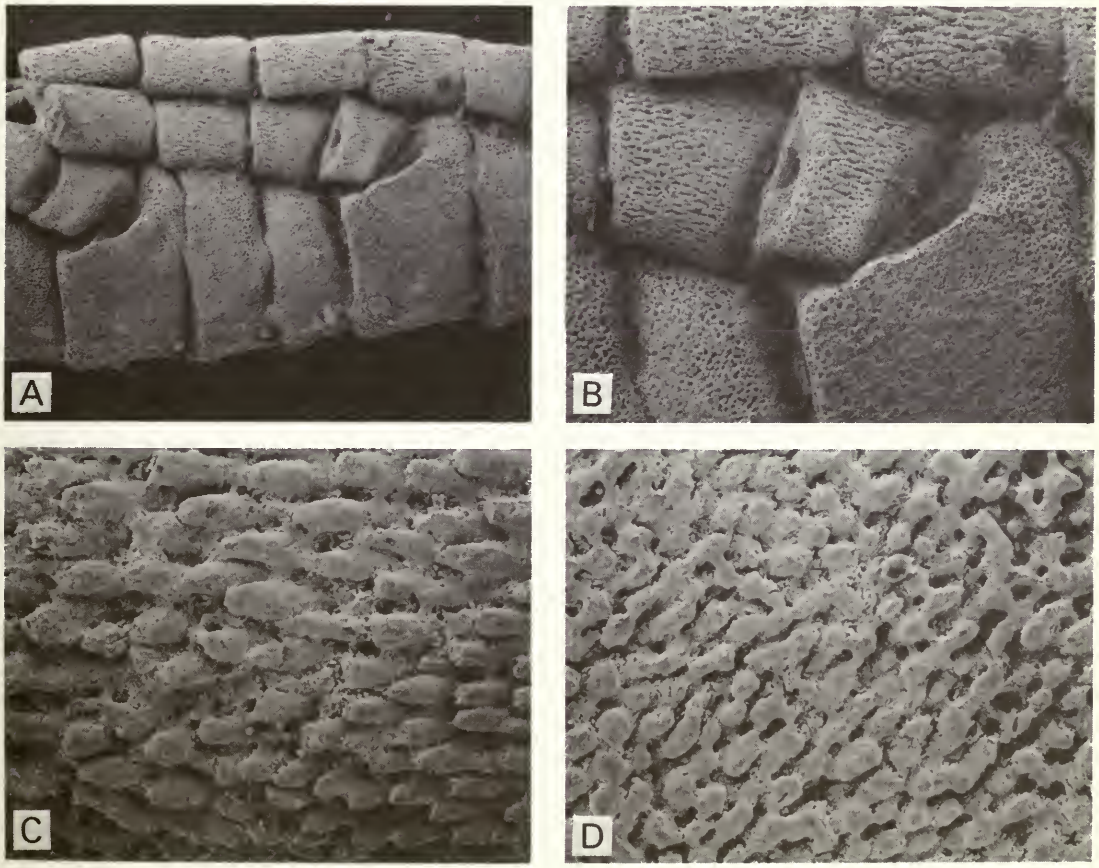


Fig. 39 Scanning electron micrographs of brachials and distal pinnules in *Ailsacrinus abbreviatus* gen. et sp. nov., BMNH E68083, Bathonian (? Sharps Hill Fm.), Eastington. A, general view; × 16·4. B, prominent aboral ligament fossa visible between first and second pinnulars; × 34. C, fascicular stereom of pinnular; × 175. D, brachial stereom; × 175.

Depending on their length, each pinnular may have two, three or even four pairs of cover plates. The stereom of cover plates is irregular and labyrinthic, with a pore diameter between 3 and 20 μm (Fig. 36B).

In some specimens of *A. abbreviatus*, pinnules situated immediately distal to the oral pinnules do not usually have preserved cover plates although they are otherwise indistinguishable from typical distal pinnules. By analogy with living comatulids (Breimer *in* Ubaghs *et al.* 1978: T43), the position of these pinnules suggest that they may have been genital pinnules.

Reconstruction

The appearance of a complete *A. abbreviatus* individual is reconstructed in Fig. 40. Of particular note is the disproportionately short stem relative to arm length.

Colour

Individuals of both *A. prattii* from Lansdown and *A. abbreviatus* from Northleach may be conspicuously coloured. Their colour varies from pale grey-purple to dusky red-purple and is usually restricted to the calyx and column. One side of the crinoid is sometimes more deeply coloured than the other (e.g. BMNH E5722) and distribution of the colour may be patchy. It seems possible that this colouration is a remnant of an original pigmentation. Living crinoids are often deeply pigmented (Hyman 1955) and, although pigmentation is fugitive (spirit-preserved specimens tend to lose their colour), it is known that organic pigments can survive fossilization in crinoids. Blumer (1960, 1962) extracted hydrocarbon pigments, 'fringelites', from U. Jurassic *Millericrinus*. He interpreted their preservation as indicating a strongly reducing environment beneath the sediment–water interface. Proof that the colouration of *Ailsacrinus* is due to similar organic pigments would necessitate time-consuming chemical analysis which has not been undertaken. However, it may be significant that the largest specimen of *A. abbreviatus* (BMNH E67807) from Northleach is also the most intensely coloured; living crinoids concentrate pigment during life and thus become more deeply coloured as they grow.

Stem ontogeny

Undoubtedly the feature of *Ailsacrinus* that has attracted most attention is the highly variable stem. Hypotheses regarding the ecology of *Ailsacrinus* must take into account stem morphology and variability. Stem morphology observable in specimens of *Ailsacrinus* is the outcome of ontogenetic processes which acted during the life of the crinoids.

It is thought that all crinoids pass through a stage during their development when they are fixed firmly to the substrate by means of a stem or column. In the cystidean and pentacrinoid stages of early ontogeny in comatulids (Breimer *in* Ubaghs *et al.* 1978), the column may possess many and well-differentiated columnals. For example, John (1938) describes a pentacrinoid of the comatulid *Notocrinus virilis* Mortensen with a crown 2·2 mm long and a 10 mm long column comprised of 45 columnals. Comatulids end their pentacrinoid stage when autotomy causes the crown to break free of the column. However, in stalked crinoids the crown remains attached to the column and a pentacrinoid stage may not be readily distinguishable (Breimer *in* Ubaghs *et al.* 1978: T56).

The early ontogeny of *Ailsacrinus* was most probably like that of comatulids, with a fixed pentacrinoid stage followed by a free-living adult stage. The duration of the fixed stage may have been short, as in comatulids, or more protracted. Kirk (1911: 49) believed that detachment took place in late ontogeny, not much earlier than crinoids represented in some of Carpenter's (1882) figures of small *Ailsacrinus* individuals. If the supposed 'root' of *A. prattii* (Carpenter 1882: pl. 1, fig. 5) is truly a holdfast, then Kirk's belief may be correct because the structure possesses apparent columnals of a moderately large size. However, in the absence of small individuals there is no way of confirming or refuting this suspicion.

Stem growth in stalked crinoids is achieved by the formation of new columnals together with accretionary growth of existing columnals (Ubaghs *in* Ubaghs *et al.* 1978: T82). *Ailsacrinus* has a homomorphic stem (nodals and internodals are not recognizable), apparently with a fused top

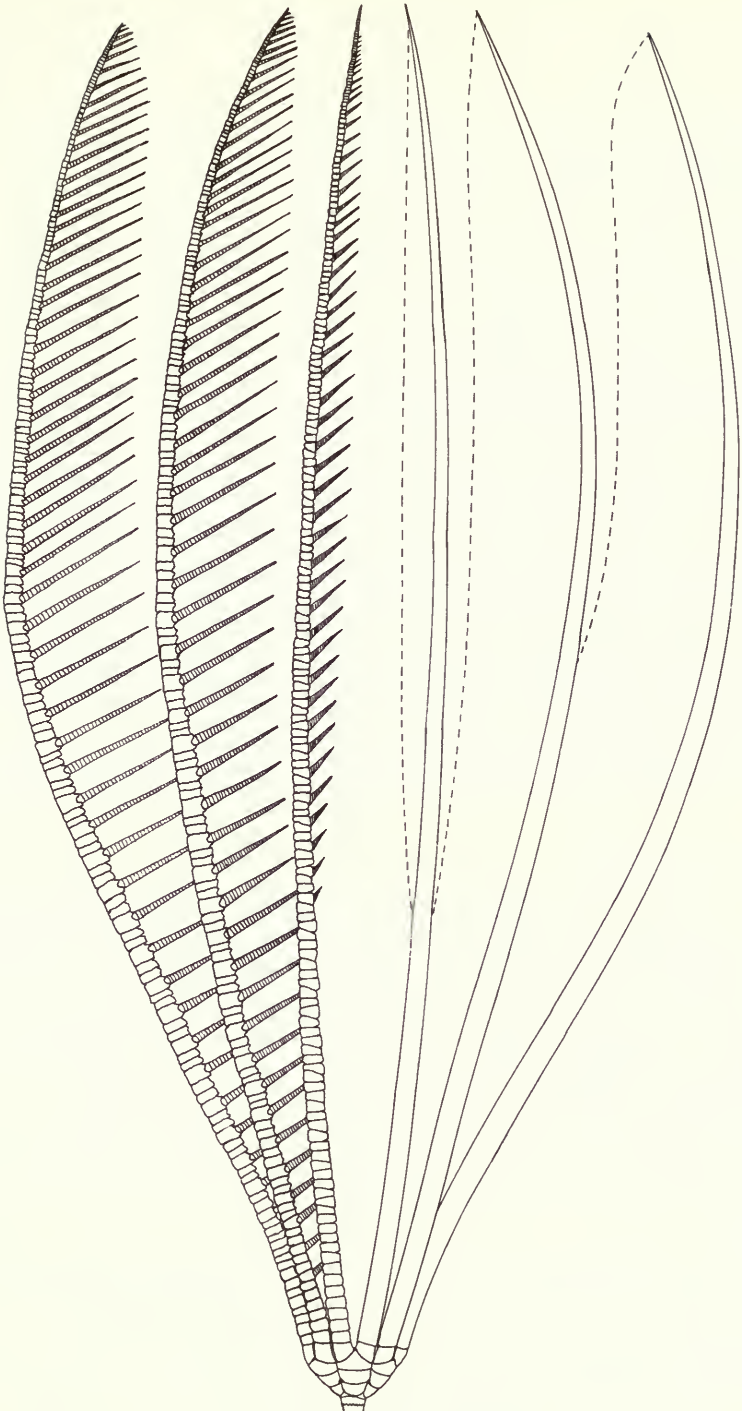


Fig. 40 Reconstruction of *Ailsacrinus abbreviatus* gen. et sp. nov. Arms have a total length of about 15–20 cm and are depicted in an arbitrary orientation which was not necessarily their position during feeding.

columnal or proximale. In this type of stem, columnal addition is localized to a generating area immediately beneath the proximale. Continued columnal addition pushes earlier columnals further down the stem and gives a proximal–distal gradient of increasing columnal age. The initial width of each new columnal is equivalent to that of the proximale at the time of columnal formation, i.e. about the same width as the base of the cup. Enlargement of the generating area during ontogeny causes new columnals to become successively wider. If this were the only factor controlling columnal width the stem would taper away from the cup. However, a second factor is the accretionary growth of existing columnals. This factor in isolation would produce a stem which tapered towards the cup because older columnals are situated furthest from the cup. Final stem-form is a result of interaction between these two factors (see Seilacher, Drozdzewski & Haude 1968). Axial growth in columnal height occurs concurrently with transverse columnal growth. If all new columnals initially had the same height, then there should be a proximal–distal gradient of increasing columnal height towards older columnals situated near the base of the stem.

Reduction in length of the stem is a further possibility in crinoids especially pertinent in the case of *Ailsacrinus*. This could result from either the shedding of whole columnals (cf. isocrinids; Rasmussen 1977) by autotomy or accident, or columnal resorption. Bather (1900: 191) said of *A. prattii* 'the crown breaks off from the root, the stem is gradually resorbed, and a free-floating stage attained'. Kirk (1911: 49) believed that the column was shortened by 'the dropping off of some of the distal columnals accompanied by more or less resorption'.

Consequently, there are three main possibilities for post-detachment stem ontogeny in *Ailsacrinus*:

1. stem lengthening by addition of columnals, and/or growth of existing columnals,
2. no change in stem length, or
3. stem shortening by shedding columnals and/or resorption.

Several lines of enquiry can be followed to decide which of these is the most likely.

Evidence from single crinoids

LENTICULAR COLUMNALS. Some individuals of both species have stems with incomplete or lenticular (Carpenter 1882) columnals. These columnals, instead of extending all the way around the circumference of the stem, when traced laterally in either direction are seen to 'pinch-out' or boudinage. They may be of slight lateral extent (Fig. 10) or may encompass most of the stem (Fig. 20A). A specimen of *A. prattii* (Fig. 20A), incorrectly drawn by Carpenter (1882: pl. 1, fig. 7), has four lenticular columnals aligned exactly above one another and alternating with complete columnals. Lenticular columnals are not exclusive to *Ailsacrinus*; de Loriol (1877–9) figured similar structures in *Millericrinus* and *Apiocrinus*.

Carpenter (1882: 33) regarded lenticular columnals as columnals in the process of formation, i.e. columnals fossilized in an early ontogenetic state. If this opinion is correct then the occurrence of lenticular columnals points to columnal addition during late ontogeny, probably after detachment.

Little is known of the process of columnal addition in crinoids. Ubaghs (*in* Ubaghs *et al.* 1978: fig. 60, 1, 2) illustrates longitudinal sections through juvenile and mature portions of the column of Silurian *Barrandeocrinus*. In the juvenile column, new columnals are present as thin discs which taper away from the column axis and are not visible at the surface. The mature column has columnals of even thickness, all reaching the surface of the column. Columnals are apparently introduced in a similar manner in articulates (Rasmussen *in* Ubaghs *et al.* 1978: T269), beginning as thin concealed discs. These immature columnals are clearly unlike the lenticular columnals of *Ailsacrinus*. Growth of lenticular columnals to completion and uniform thickness would necessitate transfer of skeletal material from adjacent thickened columnals (Fig. 41). This complication suggests that lenticular columnals are not columnals in the process of formation. Further evidence against Carpenter's hypothesis comes from the distribution of lenticular columnals which are often found distal to the expected site of columnal addition

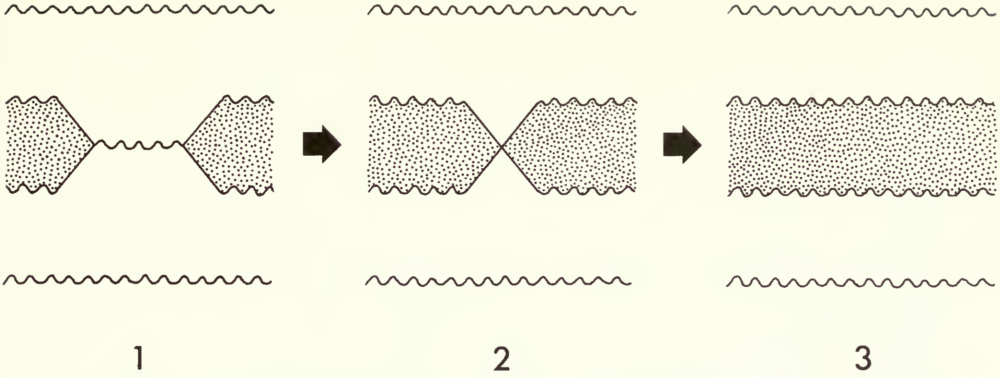


Fig. 41 Three-stage diagram showing that growth to completion of lenticular columnals of the type depicted in Fig. 20A (p. 50) would occur at the expense of adjoining columnals.

immediately beneath the proximale. Therefore, no significance can be given to lenticular columnals in stem ontogeny.

Variation in columnal size. Gradients of change in columnal size in a proximal–distal (young–old) direction are readily quantifiable in long-stemmed individuals of *A. prattii*. Turning first to columnal height, the usual pattern is one of decreasing height in a distal direction away from the cup (J33695 of Fig. 42), i.e. presumed older columnals are shorter than younger columnals. However, in at least one specimen (SM number J33694 of Fig. 42) columnal height increases away from the cup, i.e. presumed older columnals are taller than younger columnals. The occurrence of this reverse trend means that columnal height cannot be used as a reliable indicator of columnal age and provides no useful information about stem ontogeny pre- or post-detachment.

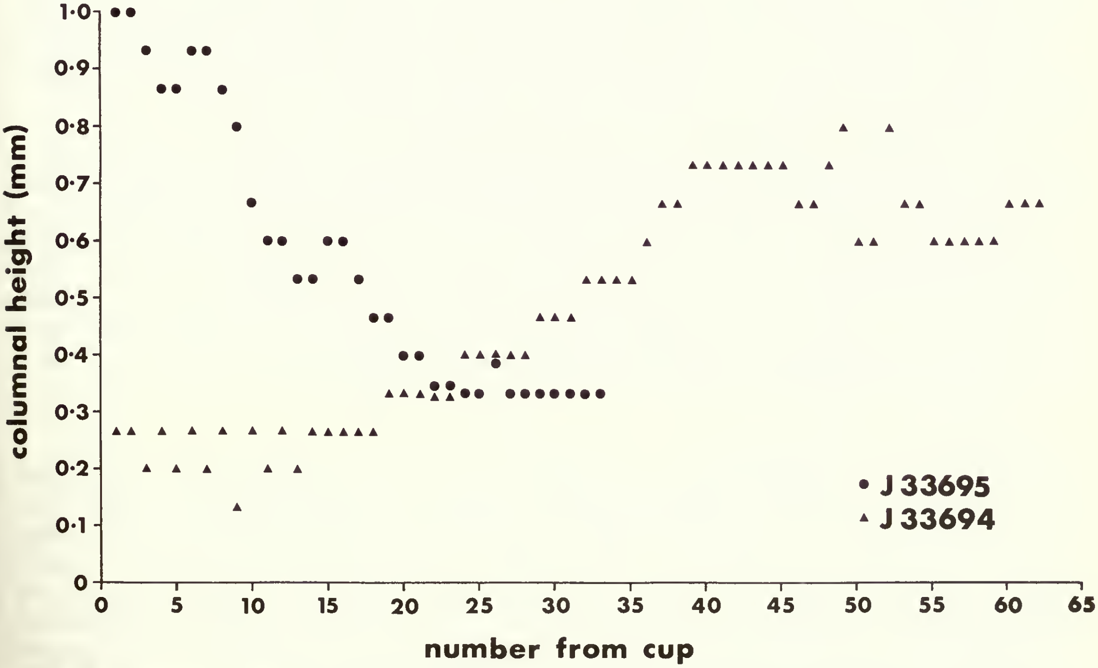


Fig. 42 Change in columnal height away from the cup in two long-stemmed individuals (SM J33695 and J33697) of *Ailsacrinus prattii* (Gray).

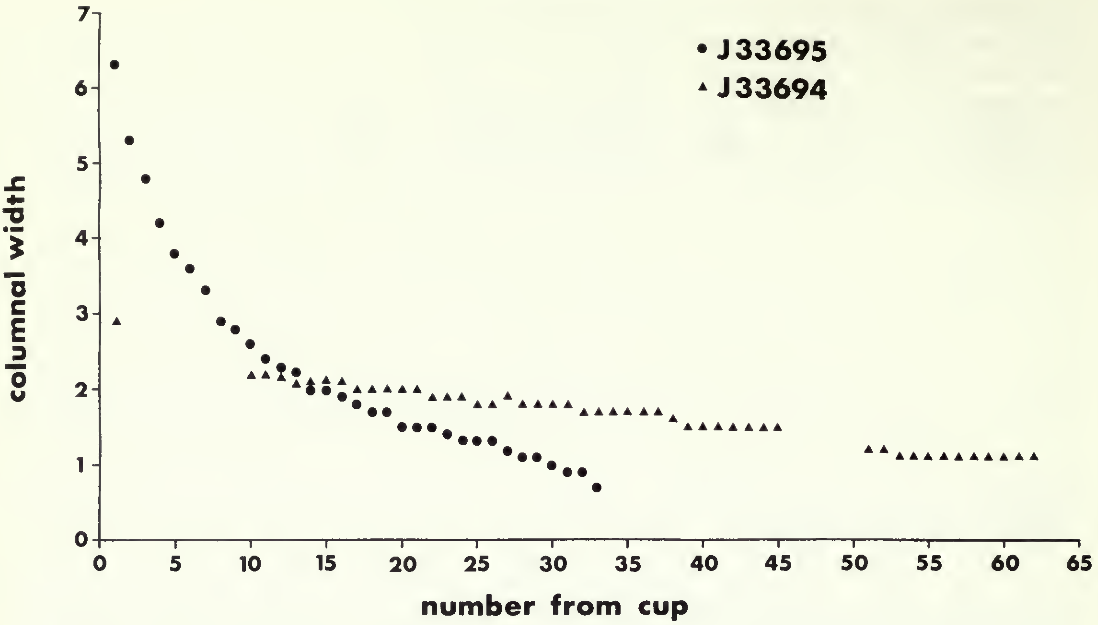


Fig. 43 Change in columnal width away from the cup in two long-stemmed individuals (SM J33695 and J33697) of *Ailsacrinus prattii* (Gray).

Columnal width always decreases away from the cup (Fig. 43), as is shown by the distal taper of *Ailsacrinus* stems. Stems with fewer columnals are generally found to taper more steeply than stems with a large number of columnals (cf. Figs 7 and 20A). If the width of columnals were proportional to the size of the generating area, then this proximal–distal size gradient would reflect addition of successively wider columnals as the crinoid grew. However, the second factor of accretionary growth after inception must be taken into account. Even if no new columnals were added after detachment, some amount of accretionary growth is likely to have occurred in order that stem width should keep pace with increasing cup width. Consequently, columnal width gradients do not help in resolving the problem of stem ontogeny.

Distalmost columnal. The columnal terminating the stem in *Ailsacrinus* most typically has a blunt, rounded end (Figs 8, 11). In some short-stemmed individuals of *A. abbreviatus*, however, the distalmost columnal has a worn quinquelobate symplectial facet (Fig. 13) which may have been a life condition rather than a result of preburial stem fracturing. The axial lumen may be exposed or occluded at the base of this columnal. It has not been possible to identify dense fabrics indicative of resorption but this may be due to poor preservation of stem stereom. However, it is clear from the general shape of the distalmost columnal that it has undergone some sort of modification, though this could be the result of any combination of post-detachment columnal growth, resorption and mechanical abrasion.

Evidence from crinoid populations

Assuming size to be a reasonable indicator of the age of a crinoid, comparisons of stem length between individuals of differing size should throw light on post-detachment ontogeny of the stem in *Ailsacrinus*. The overall size of the crinoid is impossible to determine even in these exceptionally well-preserved crinoids. A frequently employed measure of crinoid size, that of the dimensions of the dorsal cup (e.g. Roux 1978), is not suitable in *Ailsacrinus* because it is influenced by burial attitude – the cup is shortened and splayed outwards in crinoids buried upright relative to crinoids buried prostrate. In order to quantify crinoid size the dimension chosen was the height of the axillary brachial, an easily defined and measured parameter which would appear to have no causal correlative link with stem length.

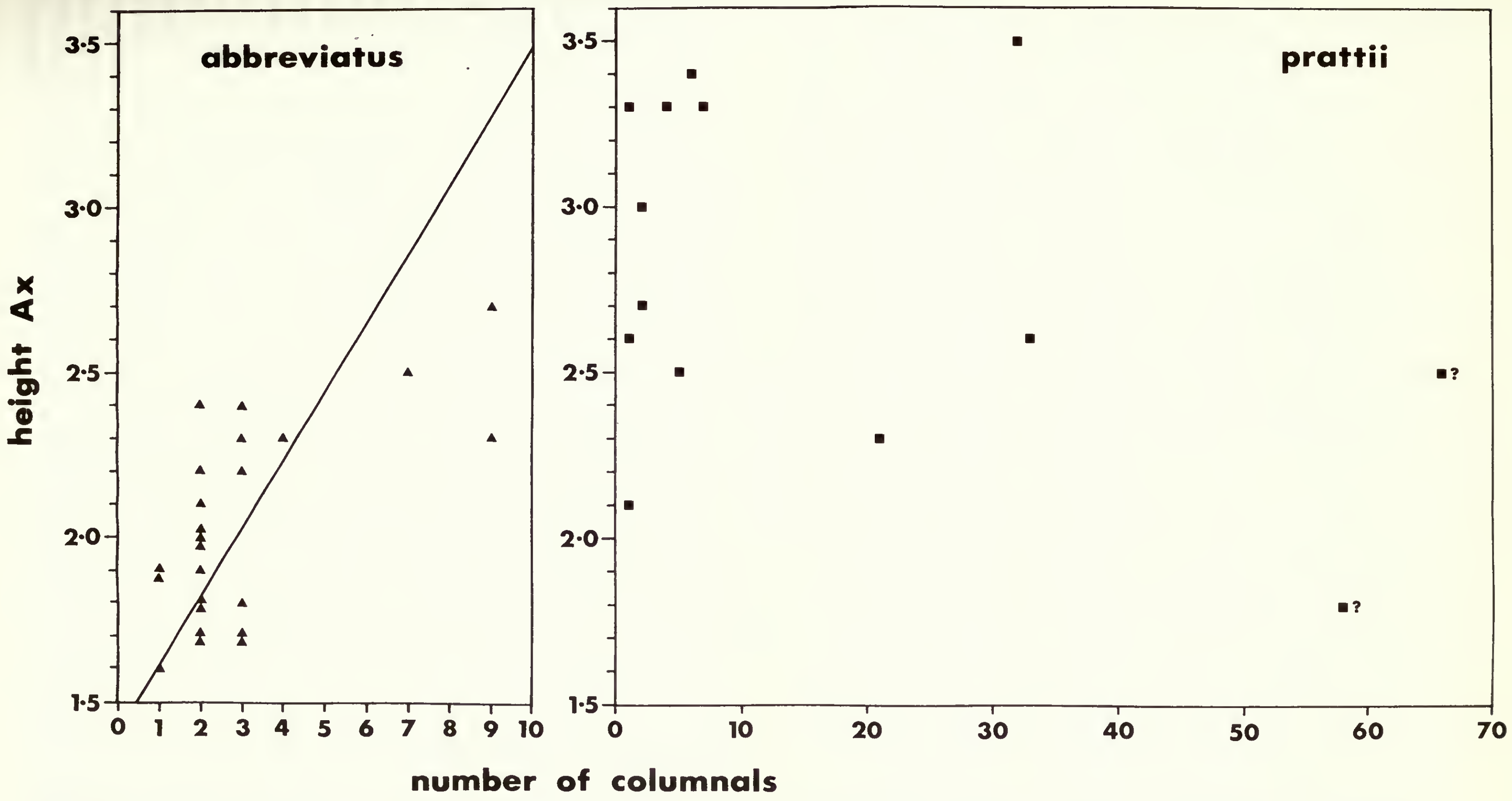


Fig. 44 Plots of crinoid size (expressed as height of the axillary brachial) against stem length (expressed as number of columnals) in 24 specimens of *Ailsacrinus abbreviatus* gen. et sp. nov. from Eastington and 14 specimens of *A. prattii* (Gray) from Lansdown Hill. Stem length is positively correlated (R = 0·652) with crinoid size in *A. abbreviatus* and the reduced major axis regression line has been fitted to the data points. There is no significant correlation (R = 0·395) between stem length and crinoid size in *A. prattii*.

Number of columnals and height of the axillary brachial were determined in 24 specimens of *A. abbreviatus* from Eastington and 14 specimens of *A. prattii* from Lansdown. These parameters were found to be positively correlated in the *A. abbreviatus* sample but not so in the *A. prattii* sample where there is a wide scatter of points (Fig. 44). Therefore, the *A. abbreviatus* data are consistent with an ontogenetic net increase in columnal number (i.e. columnal addition exceeding columnal shedding) but a similar hypothesis is not supported by data from the longer-stemmed *A. prattii*. But this result is suspect because of the probable existence of high levels of non-ontogenetic variation (e.g. in accessory plate and lenticular columnal development) within populations of *Ailsacrinus*. This non-ontogenetic 'noise' superimposed over ontogenetic variability may be responsible for the trend evident in *A. abbreviatus* and the lack of trend in *A. prattii*.

Comparison between individuals in a population is useful in discounting the possibility of ontogenetic shortening of stems by resorption of stereom more or less equally from each columnal (as opposed to resorption of the distalmost columnal only). Individuals have short stems because they have few columnals not because they have columnals of lesser height.

Conclusion

The dynamics of stem ontogeny in *Ailsacrinus* are equivocal. The presence of lenticular columnals in some stems cannot be taken as evidence for addition of columnals; proximal–distal gradients of columnal size-change are variable and can be interpreted in more than one way; distal columnals with exposed symplectial facets in *A. abbreviatus* might indicate some shedding of columnals; and crinoid size:column length comparisons within populations suggest post-detachment net addition of columnals in *A. abbreviatus* but not in *A. prattii*.

Palaeoecology

Broad environment

The Middle Jurassic sediments of southern England are predominantly carbonates. They accumulated in a shallow shelf sea where conditions were influenced by the presence of the London–Belgian Island in the east, a probable source of fresh water and terrigenous clastic material (see Ware & Windle 1981). Comparatively open, marine-shelf environments existed in the south and west during the Bathonian (for example, around Bath). Environments of the Northleach area may have often been more stressful for marine biota as a result of closer proximity to land (see Palmer 1979).

Sellwood & McKerrow (1974) discussed the stratigraphy and depositional environments of the lower part of the Bathonian in Oxfordshire and north Gloucestershire including the Northleach region. They recognized three stratigraphical divisions: Chipping Norton Formation, overlain by Sharps Hill Formation and then Taynton Limestone Formation. The fauna of the Sharps Hill Formation, in which *A. abbreviatus* probably occurs, is predominantly marine, although the presence of *Liostrea* life assemblages may indicate some salinity restriction (as, for example, some of the present day Florida Keys). Water depth is believed to have been little more than 3 m. The Sharps Hill Formation appears to grade laterally into the upper part of the Lower Fullers Earth Formation which is well-developed further south and west. This led Sellwood & McKerrow (1974) to ascribe deposition of the Sharps Hill Formation to a minor transgression which caused deeper-water sediments of Lower Fullers Earth Formation lithology to spread onto the carbonate-dominated area of north Gloucestershire and Oxfordshire.

Green & Donovan (1969) described the Great Oolite of the Bath region but did not deal with outliers north of the River Avon such as Lansdown Hill. They divided the Great Oolite sequence, from bottom to top, into Combe Down Oolite, Twinhoe Beds, Bath Oolite and Upper Rags. It is not known where the Lansdown *A. prattii* locality fits within this succession. The Bath area was apparently located on the outer part of a stable carbonate shelf. The Combe Down Oolite is interpreted as a shallow-water deposit formed by oolite deltas which flanked tidal flats with migrating channels (like the present day Trucial Coast). While the succeeding

Twinhoe Beds may have been deposited in quieter and rather deeper water, the Bath Oolite seems to make a return to conditions similar to those inferred for the Combe Down Oolite. The Upper Rags may represent a more varied depositional regime. Analysis of a single bed exposed on Bathampton Down (Elliott 1974) suggests that it accumulated on a current-swept, inter-reef seafloor like some modern environments which exist in water 30–60 m deep off the Capricorn Islands (Great Barrier Reef) and the Bermudas.

The Eastington crinoid bed

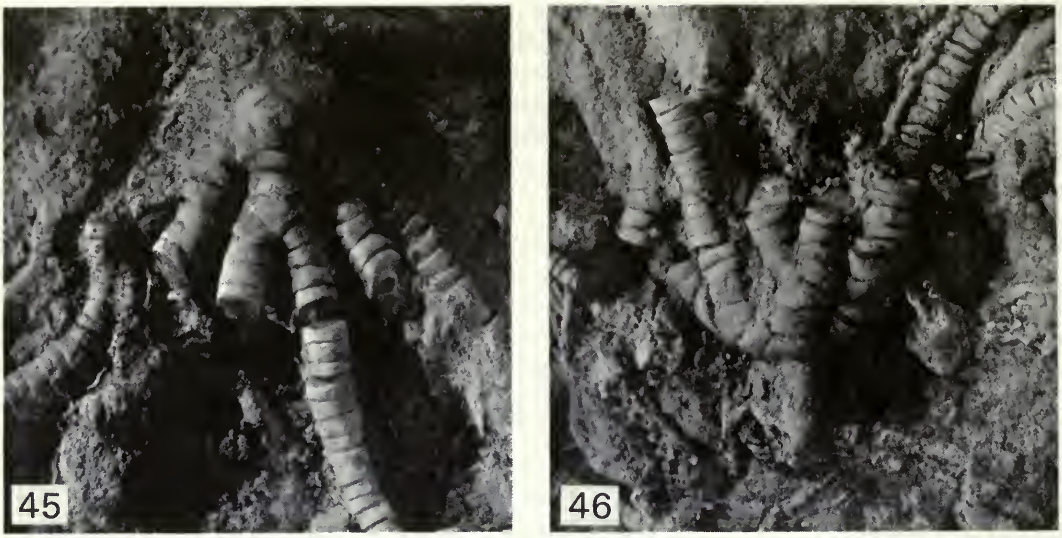
A detailed study has been undertaken of the *A. abbreviatus* bed from the new locality near Eastington. Within the confines imposed by poor exposure, this has allowed a tentative model to be proposed for the genesis of the Eastington crinoid bed incorporating sedimentological, palaeoecological and taphonomic inferences.

LITHOLOGY. The well-sorted bio-oosparite (Fig. 3, p. 41) comprising the bulk of the bed is clean-washed and was undoubtedly formed, although not necessarily deposited, in a comparatively agitated environment. Features indicating a storm deposit ('tempestite' of Ager, 1974), such as matrix-supported intraclasts, are notably absent. The subparallel orientation of shell fragments (Fig. 3A) suggests grain by grain deposition rather than the nearly instantaneous deposition caused by a storm. The thin muddy layers which drape each fossiliferous bedding plane stand in marked contrast to the bio-oosparite. The major clay mineral present in this mud is illite; there are no clay minerals which may be interpreted as having a volcanogenic origin. This is important because elsewhere in the British Jurassic, Ali (1977) has postulated smothering by volcanic ash as a source of catastrophic mortality of corals. Survival of discrete muddy layers without mixing with the clean-washed carbonate sediment suggests that the mud was stabilized during carbonate deposition. Stabilization of mud in Recent sedimentary environments is commonly achieved by the presence of an algal mat or other organic film (e.g. Bathurst 1975: 122).

SEDIMENTARY STRUCTURES. Bioturbation is absent from the crinoid bed and this is true for the Sharps Hill Formation in general (Sellwood & McKerrow 1974). Burrowing animals, whose activities would probably have disarticulated the buried crinoids, may have been excluded by rapid deposition (Sellwood & McKerrow 1974) or by unfavourable anaerobic conditions beneath the sediment surface (cf. Rosenkranz 1971). The existence of anaerobic conditions is supported by apparent pigment preservation in *A. abbreviatus*; Blumer (1960) ascribes preservation of organic pigments in fossil crinoids to the presence of strongly reducing conditions. This in turn is consistent with the possibility of an organic film stabilizing the muddy sediment.

Traces of symmetrical ripples occur near the top of the crinoid bed. These wave-generated bedforms would have been produced in shallow water above wave base.

CRINOID PRESERVATION. Most specimens of *A. abbreviatus* are exceptionally well preserved, lacking post-mortem abrasion and with delicate structures (e.g. pinnule cover plates) usually intact and unbroken. The crinoids are well-articulated, especially near the base of the bed. The overlying shell lag deposit contains short, articulated fragments, possibly reworked from the crinoid bed below. Where arms are disarticulated, the amount of dislocation between the disarticulated portions tends to be small. Similar preservation in other fossil crinoids is generally attributed to rapid burial *in situ* or with very minor transportation (e.g. Brett 1978, Brower 1973, Hess 1972, 1973). Aslin (1968) also suggests rapid burial to account for good preservation of echinoids in rocks of Middle Jurassic age in Northamptonshire. Working with living crinoids, Cain (1968: 192) found that, within two days of death, specimens of *Antedon bifida* in still water 'collapsed into a mass of arms and cirrus fragments'. Similarly, comatulids studied by Liddell (1975) were completely disarticulated within two days of death when placed in an agitated environment but crinoids buried and then exhumed after six days were well-preserved and retained their colour. However, considerable interspecific variation in the disarticulation rates of Recent crinoids and ophiuroids was found by Meyer (1971). Scavenging organisms played an important role in the disarticulation process. These studies on living crinoids provide strong



Figs 45–46 *Ailsacrinus abbreviatus* gen. et sp. nov., Bathonian (? Sharps Hill Fm.), Eastington. Fig. 45, BMNH E67807, short-stemmed crinoid in an upright orientation on the underside of a bedding plane; ×2·3. Fig. 46, BMNH E67817, long-stemmed crinoid lying prostrate on a bedding plane; ×1·9.

evidence for rapid burial of individuals of *A. abbreviatus*. This probably occurred while the crinoids were still alive or, less likely, shortly after death. Transport of dead crinoids over significant distances can be discounted but it is possible that they were swept to their burial site before death.

Crinoid orientation. Over 50% of the crinoids studied are preserved in presumed life-position, i.e. with their adoral surfaces facing upwards. In these individuals the arms diverge radially from the cup (Fig. 25, p. 52) and lie parallel or almost parallel to the bedding. The short stem is orientated perpendicular to the bedding (Fig. 45). About 40% of the crinoids are prostrate, typically with arms close together and arms and stem parallel or subparallel to the bedding (Fig. 46). Some individuals are obliquely orientated and a few are upside down. There is no discernible alignment of prostrate crinoids or groups of arms on the bedding planes. Tangling of arms is rare despite high concentrations of specimens. Many arms are bent, flexed either aborally or adorally. Some bent arms extend upwards through a few centimetres of sediment.

This orientational evidence shows that at least some of the crinoids were disturbed from their presumed life positions before or during burial. The arms of partially buried crinoids are unlikely to have projected above the sea-bed for very long before disarticulating. The occurrence of arms orientated at high angles to the bedding thus again suggests rapid deposition, and their lack of alignment that the crinoids were not buried in a regime of strongly directional currents.

Population density. The mud-draped bedding planes are characterized by a high density of crinoids, exceeding 200/m^2 in some instances. High population density may be attributed to concentration by currents or burial of a densely aggregated living population. Dense aggregations of fossil crinoids, so-called 'crinoid gardens' (Moore & Teichert *in* Ubaghs *et al.* 1978: T8), are well known among pelmatozoic species (e.g. Brower 1973, Brett 1978). Highly aggregated populations are also a feature of some Recent comatulids (see Reese 1966; Breimer *in* Ubaghs *et al.* 1978: T328); Marr (1963) for example illustrates an Antarctic sea-bed densely colonized by comatulids. According to Keegan (1974), *Antedon bifida* may achieve population densities of 1200/m^2 on the west coast of Ireland. Aggregation may arise from poor larval dispersal, selection of favourable habitats already populated by conspecifics, or truly gregarious behaviour (preferential settlement of larvae close to conspecifics). The advantages of aggregation have been considered by Warner (1971, 1979). He notes that it is likely to promote cross-fertilization, increase stability in current-swept areas, allow the mutual support of arms raised in suspension feeding and enhance settlement of food particles from suspension because a mass of individuals forms an effective current baffle. Wilson, Holme & Barratt (1977) suggest protection from predation as a further advantage of aggregation in echinoderms. It is difficult to discount conclusively concentration by currents as the cause of high population density in *A. abbreviatus*, but the alternative hypothesis of burial of an aggregated living population is more appealing in view of the analogues which exist among comatulids at the present day.

Population variability and structure. Variation in axillary brachial height, used as a convenient indicator of crinoid size (see p. 62), shows the variability of *A. abbreviatus* in the Eastington crinoid bed (Fig. 47). A sample of 128 crinoids derived from various parts of the bed has a size frequency distribution which is almost normal. In contrast, a subsample of 37 crinoids on a single bedding plane has a negatively skewed distribution. Interpretation of these patterns of distribution can be made either on the premise that they show variation within a population of

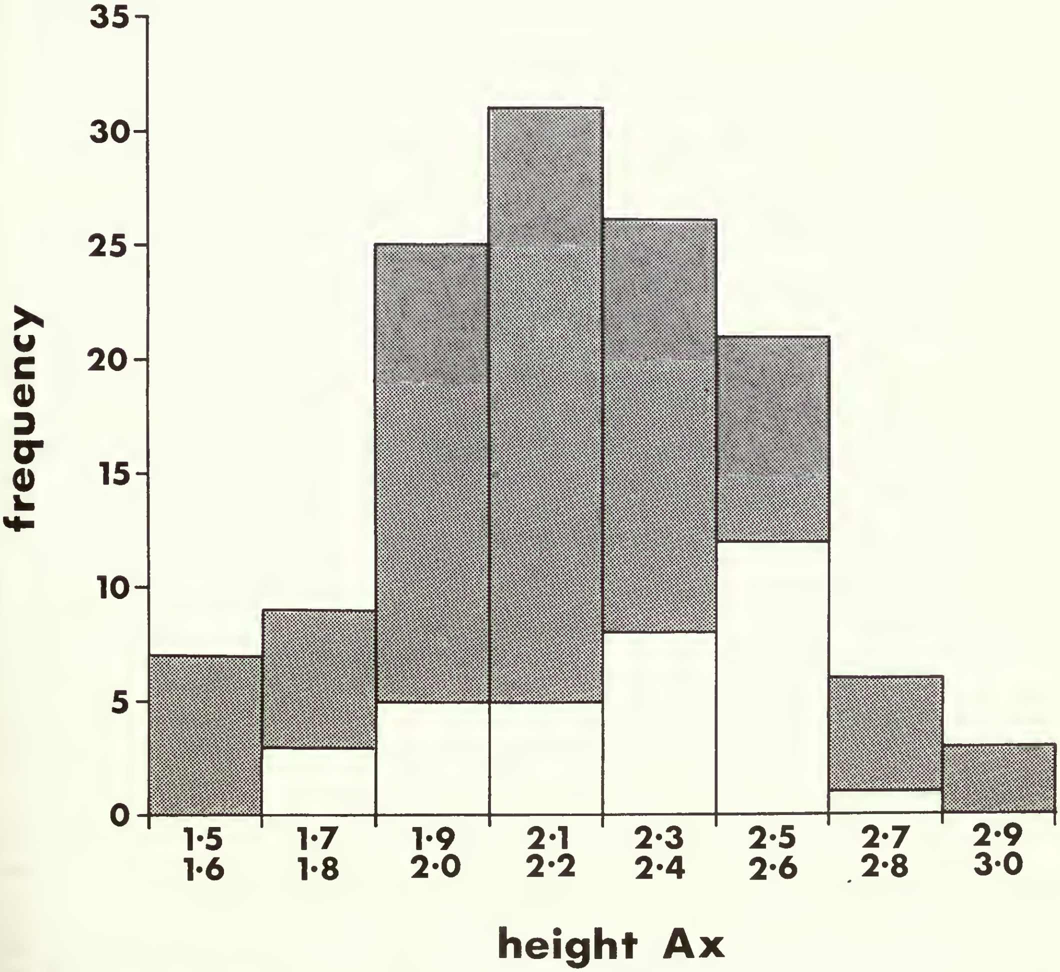


Fig. 47 Frequency histogram of crinoid size (expressed as height of the axillary brachial in mm) in 128 individuals of *Ailsacrinus abbreviatus* gen. et sp. nov. from the Bathonian (? Sharps Hill Fm.) of Eastington. A subsample of 37 individuals from a single bedding plane is unshaded.

equal-aged individuals, or that size reflects age and the distribution reveals the demographic structure of the crinoid population. In reality, the distribution is likely to be the result of a combination of these non-ontogenetic and ontogenetic factors. However, for present purposes it will be assumed that ontogenetic factors predominate and the data will be analysed accordingly.

Hallam (1972) reviewed the interpretation of population structure in fossils. He distinguished between living populations and death assemblages, each of which is likely to produce a different type of size frequency distribution. The size frequency histogram for a living population is very often polymodal because recruitment to the population tends to be episodic (e.g. seasonal), giving distinct age/size classes. For death assemblages a unimodal distribution is more probable and the shape of the distribution is dependent largely on rates of growth and mortality. Benthic assemblages usually have positively skewed distributions due to high juvenile mortality, while normal distributions are unusual, and negatively skewed distributions highly exceptional.

The size frequency distribution of *A. abbreviatus* fits neither that typical of a living population (though population structure in crinoids specifically may be unknown) nor that typical of a death assemblage. If the model proposed below for the formation of the Eastington crinoid bed is correct, then the crinoids represent a succession of living populations which were catastrophically buried. The size frequency distribution of the large sample of crinoids from throughout the bed may be a mixture of several living populations. However, that of crinoids on a single bedding plane could reflect the structure of a single population. This is a negatively skewed distribution; large, presumed old, individuals are over-represented. Such a population structure is consistent with continuous recruitment of adult crinoids into the population following a period of attached life elsewhere. Assuming growth rate to have decreased during ontogeny, the proportion of large crinoids in the population would increase with time, yielding a negatively skewed size frequency histogram.

TENTATIVE MODEL OF CRINOID BED FORMATION. Evidence for rapid sediment-deposition and disturbed crinoid burial seems clear. The sediment responsible for crinoid burial appears to have been the clean-washed carbonate sand rather than the mud of the bedding-plane drapes. Significant transport of crinoids before burial is thought unlikely and sediment inundation of densely-aggregated living populations *in situ* or very locally transported seems more probable. A multi-event model seems more compatible with the evidence than a single event model. This model can be summarized as follows:

1. Colonization of the sea-bed by crinoids and deposition of muddy sediment in fairly quiet water aided by the baffling action of the crinoid arms. Once deposited, the mud may have been stabilized by an organic film which also promoted anaerobic conditions within the sediment and precluded infauna whose activities may otherwise have disarticulated crinoids already buried. Adult crinoids were recruited into the densely aggregated crinoid population by migration from sites of attachment located elsewhere.
2. Rapid influx of clean-washed carbonate sand generated in a higher energy environment and possibly introduced by tidal currents. Some of the crinoids were buried immediately and retained their upright life-orientation, but others were disturbed from their life-orientation, locally transported, and buried prostrate or upside down.
3. Return to normal conditions with recolonization by crinoids and recommencement of mud sedimentation.
4. Repetition of this sequence of events to give the full thickness of the crinoid bed.
5. Change in the sedimentary regime signalled by the deposition of a cross-bedded shell lag over the crinoid bed, perhaps due to the advance of a dune field.

Stem function

Inference of stem function is important in understanding the mode of life of *Ailsacrinus*. As there are no living crinoids of known ecology which have a stem morphology similar to that of *Ailsacrinus*, a functional morphological approach has been applied to the problem of stem function (Rudwick 1961).

Potential functions of the stem in *Ailsacrinus* are:

1. as a column to hold the crown aloft;
2. as a means of attaching the crinoid to the substrate;
3. as ballast to stabilize the crinoid;
4. as a counterpoise to keep the crinoid in an appropriate orientation; or
5. without function, at least during the unattached period of life.

COLUMN. The paradigm for a column functioning to elevate the crown is a stout structure with little flexibility between columnals, thickened at its base where stresses caused by horizontal water-movements could be concentrated, and flat-bottomed or firmly attached to the substrate by some means. This paradigm, approached in articulates such as *Apiocrinites* (Breimer & Lane *in* Ubaghs *et al.* 1978: T334), is clearly not fulfilled by *Ailsacrinus*.

ATTACHMENT. Attachment structures or holdfasts are part of the fossilizable skeleton in various crinoids. Alternative but equally viable solutions to anchoring the crinoid are provided by different types of holdfast fitted to soft substrates, hard bottoms, substrates with a complex relief, etc. (see Brett 1981). Paradigms for attachment generally involve structures of expanded surface area (e.g. cemented bases or divided distal ends of the stem) and/or with the ability to grasp (e.g. comatulid cirri). It seems clear that the stem of *Ailsacrinus* lacked any adaptation for attaching the crinoid.

BALLAST. The function is fulfilled by any structure denser than sea-water. The optimal weight of ballast required might be expected to vary according to the unknown factors of net crinoid buoyancy and strength of environmental water currents. Therefore, it is difficult to assess the possible role as ballast of the stem in *Ailsacrinus*.

COUNTERPOISE. The paradigm for a counterpoise structure providing stability has a low centre of gravity close to the substrate. This is well illustrated by the stemless inadunates *Agassizocrinus* (Ettensohn 1975) and *Paragassizocrinus* (Ettensohn 1980), which have heavily-calcified infra-basal cones giving them a 'roly-poly doll' construction. The counterpoise paradigm may be approached adequately in some very short-stemmed individuals of *Ailsacrinus* but it is certainly not fulfilled in long-stemmed individuals of *A. prattii* where the centre of gravity is likely to have been located in the proximal part of the stem some way above the substrate.

FUNCTIONLESS. To argue effectively that a structure is functionless it is necessary to eliminate all possible functions. This is clearly impossible if only for the reason that not every function may have been conceived. However, a hypothesis which deserves consideration for *Ailsacrinus* is that the stem was functional (e.g. for attachment and crown elevation) during the attached stage of ontogeny but essentially functionless when the free-living stage was reached. In Recent isocrinids (Rasmussen 1977) the long cirriferous stem may fracture at the cryptosymplexy beneath a nodal, leaving the crown and proximal part of the stem to drift away before becoming re-attached elsewhere. Stem fracturing may represent true autotomy or, as believed by Rasmussen, breakage in response to water movements or other external forces. A similar process of stem fracturing, but without subsequent cirral reattachment, may be envisaged for *Ailsacrinus*, perhaps at a late stage in ontogeny (see above). If caused by external pressure, stem breakage may have left individuals with stems of widely varying length. Thereafter, individuals possibly lacked the ability to shorten the stem and relied on occasional accidental shedding of columnals.

Feeding ecology

Present interest in the feeding ecology of living and fossil crinoids focuses on an apparent polarization into current-seeking rheophiles and current-avoiding rheophobes (Breimer 1969, Breimer & Lane *in* Ubaghs *et al.* 1978: T333). Rheophiles, present among Recent stalked crinoids and comatulids, commonly form brachial filtration fans (Magnus 1967). The arms are spread in a paraboloid with their adoral surfaces pointing upcurrent. A radial feeding posture is less common. Rheophobes, possibly a minority of living crinoids, include deep water comatulids

(Pérès 1958, 1959) in which the arms form a collecting bowl for feeding on the plankton rain. However, there may be considerable variation in feeding behaviour within some species and the ecological dichotomy into rheophiles and rheophobes may break down. For example, La Touche (1978) observed that flexibility in the arm movements of *Antedon bifida* allowed individuals to feed in diverse current regimes. In slack water, animals most commonly held their arms in an inverted cone. Animals in current speed of up to 30 cm/s held their arms in the shape of a bent-over, flattened cone.

Breimer & Lane (*in* Ubaghs *et al.* 1978) discuss features of the stalk and arms useful as a guide to inferring the palaeoecology of fossil crinoids. Species of *Millericrinus* with a rudimentary stem (evidently referring to *Ailsacrinus*) they consider (1978: T334) to be benthic rheophobes. Certainly it is difficult to envisage *Ailsacrinus* forming a radial brachial filtration fan for rheophilic feeding; the stem is not long enough to hold the crown high enough aloft. The lack of anchorage structures seems to be another problem. Individuals lack grasping cirri and also hooks or spines on the arms and pinnules which are used for attachment in some comatulids (e.g. *Comanthina schlegeli*) that secondarily lose their cirri (Meyer & Macurda 1977). However, not all rheophiles form brachial filtration fans and, if *Ailsacrinus* lived in dense populations, stability may not have necessitated direct attachment to the substrate. Ecological analogies may be valid with the living brittle star *Ophiothrix fragilis* (see Warner 1979). Like *Ailsacrinus*, *O. fragilis* is a suspension feeding echinoderm living in dense aggregations composed of individuals lacking a means of direct attachment to the sea bed. Arms of individuals are stretched upwards into the current and interlock to form a mat stable in velocities exceeding 20 cm/s. Aggregations are probably maintained by preferential settlement of larvae around adults, combined with the ability of dislodged adults to locate aggregations and walk towards them.

To summarize, *Ailsacrinus* may have been either a rheophobic or rheophilic suspension feeder living in dense populations. Recruitment into these crinoid mats seems to have taken place by immigration of individuals which had attained an adult size during a protracted period of attached ontogeny spent elsewhere. The active locomotory abilities of *Ailsacrinus* were perhaps limited; arms are robust and muscular fossae small. Migration was more likely achieved by passive drifting or comasterid-like crawling than by antedonid-like swimming. This ecological model, devised largely using evidence from *A. abbreviatus*, may or may not apply to *A. prattii*.

Evolution

Phylogenetic affinities

The Articulata are divided into seven orders by Ubaghs (*in* Ubaghs *et al.* 1978: T364): Millericrinida, Cyrtocrinida, Bourgueticrinida, Isocrinida, Comatulida, Uintacrinida and Roveacrinida. Evolutionary relationships between these orders are poorly understood (see Rasmussen *in* Ubaghs *et al.* 1978: T302–5; Pisera & Dzik 1979). Although articulate crinoids are usually considered to have evolved from the Poteriocrinina, a group of dicyclic Palaeozoic inadunates, their structural diversity is taken by some to suggest a polyphyletic origin (Ubaghs *in* Ubaghs *et al.* 1978: T281).

Cyrtocrinids, bourgueticrinids, uintacrinids and roveacrinids are well-defined and morphologically distinctive groups which can be eliminated from any discussion of the affinities of *Ailsacrinus*. This leaves the millericrinids, isocrinids and comatulids, all of which are known in deposits of Bathonian age. Millericrinids are characterized by the presence of a proximale and a lack of cirri. The column typically forms a conical transition to the cup. Nodals are absent, although the alternately large and small columnals in *Angulocrinus* (Rasmussen *in* Ubaghs *et al.* 1978: fig. 550,2) resemble nodals and internodals respectively. Isocrinids possess nodals and cirri but lack a proximale. Comatulids have a reduced stem consisting of a single cirriferous centrodorsal or, in early forms, a few reduced nodals (Hess 1951). Previously, *Ailsacrinus* (as *Millericrinus prattii*) has been assigned to the millericrinids.

Table 1 summarizes the principal morphological characters shared by *Ailsacrinus* with typical millericrinids, isocrinids and comatulids. These characters are discussed in turn below.

Table 1 Morphological characters shared by *Ailsacrinus* with Millericrinida, Isocrinida and Comatulida.

	Ailsacrinus	Millericrinida	Isocrinida	Comatulida
Stem	reduced	large	large	reduced
Proximal columnal	fused	fused	free	fused
Cirri	absent	absent	present	present
Basals	reduced	large	reduced	reduced
Oral pinnules	present	absent	absent	present
Syzygies	present	absent?	present	present

STEM. A reduced stem, shared by *Ailsacrinus* and comatulids, is presumably an advanced character but is not a reliable synapomorphy because stem reduction has undoubtedly occurred several times during crinoid evolution (see Kirk 1911). Furthermore, reduction of the stem to a single centrodorsal in comatulids seems to have been the result of columnal fusion, a process for which there is no evidence in *Ailsacrinus*.

PROXIMAL COLUMNAL. A fused proximal columnal is present as a proximale in *Ailsacrinus* and millericrinids, and as a centrodorsal in comatulids. Although fusion may be an advanced character and is absent in isocrinids, homology between the proximale of *Ailsacrinus* and the centrodorsal of comatulids is unlikely because the former is united to the cup by a symplectial articulation and the latter by a synostosial articulation.

CIRRI. By outgroup comparison with poteriocrininids, cirri may be a primitive character of the Articulata. If so, absence of cirri is an advanced character shared by *Ailsacrinus* and millericrinids. Character absences may, however, be unreliable indicators of phylogenetic affinity.

BASALS. Reduced basals are shared by *Ailsacrinus*, isocrinids and comatulids. Despite the fact that small basals may be an advanced character state (by outgroup comparison), basal reduction is a comparatively simple process with a high probability of occurring more than once. If so, reduced basals are not a good synapomorphy.

ORAL PINNULES. Among living crinoids, oral pinnules are said to be restricted to comatulids (Breimer *in* Ubaghs *et al.* 1978: T43). They appear not to have been described from non-comatulid articulates prior to this account of *Ailsacrinus*. The fine structure of oral pinnules in *Ailsacrinus* differs somewhat from those of comatulids. Oral pinnules of the antedonid *Promachocrinus* are slender, with long, elongate pinnulars (Breimer *in* Ubaghs *et al.* 1978: fig. 28,4), whereas those of comasterids possess distinctive distal pinnulars equipped with teeth to form terminal combs (Breimer *in* Ubaghs *et al.* 1978: fig. 28,3). In *Ailsacrinus* the pinnulars are short and high, and lack terminal combs. The phylogenetic significance of oral pinnules in *Ailsacrinus* is difficult to assess because of this disparity in detailed structure, and because oral pinnules may be present in other fossil millericrinids but have not been recognized owing to inferior preservation. The extant millericrinid suborder Hyocrinina provides no help in resolving this problem because these living crinoids are devoid of pinnules on their proximal brachials.

SYZYGIES. Syzygies are well-developed in *Ailsacrinus* and, as in comatulids, the hypozygals lack pinnules. The frequency of syzygies along the arms of *Ailsacrinus* is similar to that of comatulids. However, the first syzygy in *Ailsacrinus* occurs between secundibrachs 4 and 5 whereas the usual position for this ligamentary articulation in comatulids is between secundibrachs 3 and 4. There are clear differences in stereom ultrastructure between the syzygial facets of *Ailsacrinus* and comatulids, those of *Ailsacrinus* having a subconcentric fascicular fabric. Although Rasmussen (*in* Ubaghs *et al.* 1978: T817) states that syzygies are absent in millericrinids, facets of disarticulated brachials from another millericrinid, *Apiocrinites*, often bear a pattern of radiating ridges suggestive of a syzygial articulation. Furthermore, the occurrence of

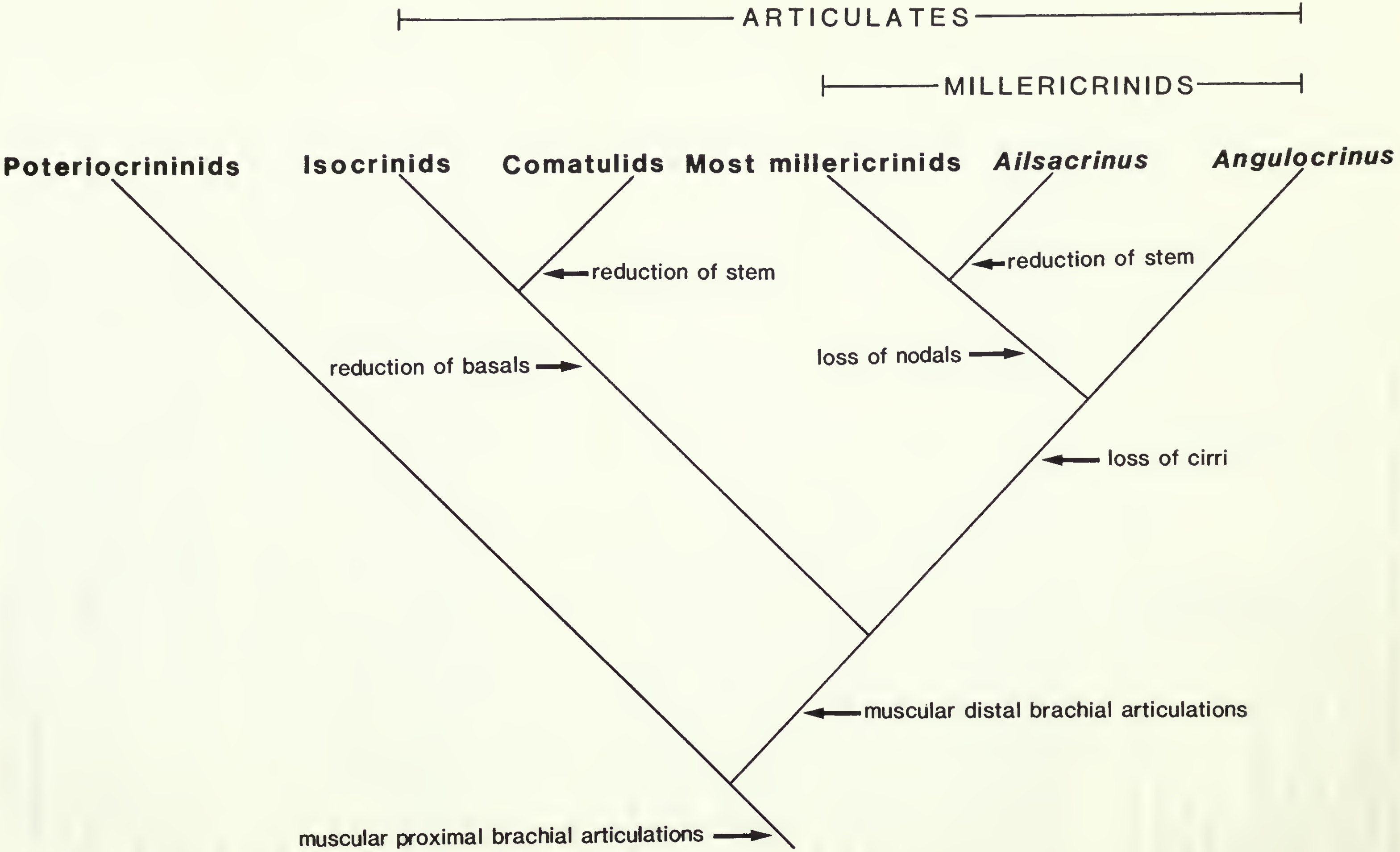

ARTICULATES
MILLERICRINIDS
Poteriocrininids
Isocrinids
Comatulids
Most millericrinids
Ailsacrinus
Angulocrinus
reduction of stem
reduction of stem
reduction of basals
loss of nodals
loss of cirri
muscular distal brachial articulations
muscular proximal brachial articulations

Fig. 48 Tentative cladogram showing inferred relationships between *Ailsacrinus* gen. nov. and some other crinoids.

possible syzygies in certain poteriocrininids (Strimple *in* Ubaghs *et al.* 1978: T301) suggests that they may be a primitive character of articulate crinoids and of no value in deciding relationships in the group.

The foregoing discussion serves to highlight the acute need for more information on the morphology of articulates, especially their brachial articulations and pinnule structure. Until this is forthcoming, relationships within the group will remain obscure. Therefore the favoured cladogram (Fig. 48) showing the relationships between *Ailsacrinus* and other articulates is very tentative. *Ailsacrinus* is here interpreted as a millericrinid possessing autapomorphies (reduced stem and basals, oral pinnules, well-developed syzygies) resulting in a morphology convergent with comatulids.

Adaptive evolution

When discussing the post-Palaeozoic evolution of crinoids, Meyer & Macurda (1977) focused on the impressive adaptive radiation shown by the Comatulida. They considered articulates to be pre-adapted for an eleutherozoic existence because they possess muscular arms which are potentially of value in crawling and swimming, as in comatulids. Active locomotion is used by comatulids to seek favourable habitats and to avoid stress. Meyer & Macurda (1977) identified predator stress, imposed by diversifying teleost fish, as an important selective factor during comatulid evolution.

In view of the similar time of origin of comatulids (known from the Toarcian) and *Ailsacrinus*, it is tempting to explain the origin of *Ailsacrinus* in identical terms. However, eleutherozoic lifestyles may have characterized many other extinct crinoids and seem to have arisen several times among Palaeozoic taxa. These Palaeozoic crinoids were neither pre-adapted in the sense of having muscular arms nor subjected to the predator stress of teleosts. The origin of both comatulids and *Ailsacrinus* in Jurassic times may be quite coincidental.

Temporal trends of morphological change apparent within the genus *Ailsacrinus* are the opposite of those expected. The older species, *A. abbreviatus*, resembles less the putative stalked ancestor of the genus than does the later *A. prattii*, which usually has a longer stem and altogether more bulky morphology. Early notions of *Ailsacrinus* were of a crinoid evolving towards a fully eleutherozoic lifestyle by elimination of the stem. The modest evidence from the two known species fails to support this hypothesis.

Of *Millericrinus prattii*, Kirk (1911: 49) said '. . . were *Millericrinus* to have possessed cirri, there is small doubt that this very species would have formed the radicle of a line essentially comatulid in habit, and perhaps of considerable vigor.' This viewpoint remains an appropriate epitaph for an ecological excursion by the millericrinids into an eleutherozoic lifestyle which proved unsuccessful in terms of duration and taxonomic fecundity.

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Glossopteris anatolica sp. nov. from uppermost Permian strata in south-east Turkey

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Synopsis

A full description is given of the leaf impressions recorded in 1962 as *Glossopteris* cf. *stricta* Bunbury from the Hazro flora in south-east Anatolia. Comparisons are made with several species from India, South America (Patagonia) and Antarctica. *Glossopteris anatolica* is regarded as an immigrant from the Gondwana Realm which reached the equatorial belt in latest Permian times. The composition of the Hazro flora is commented on in the light of a current revision.

Introduction

The presence of Gondwana elements in the Late Permian flora of Hazro in south-eastern Anatolia, Turkey, which is predominantly of Cathaysian affinity, has been reported by Wagner (1959, 1962). Most important in this respect was a species of *Glossopteris* which was compared with the Indian Gondwana species *G. stricta* Bunbury. Plumstead (in Discussion of Wagner 1962) criticized the identification and hinted strongly at the possibility that homeomorphy might have given rise to leaf shapes and venations similar to those of *Glossopteris* from Gondwanaland. The identification as *Glossopteris* was supported by Lacey (in Discussion of Wagner 1962) and by Archangelsky & Arrondo (1970: 81, footnote). Asama (1976: 203), on the other hand, regarded 'the plant reported from the Hazro flora as *Glossopteris* . . . to have been derived from the Euramerian plant *Lonchopteris* by Enlargement.' There is a marked difference between the fernlike fronds of the pteridosperm *Lonchopteris* and the *Glossopteris* type leaves of the Hazro region. The reference to Enlargement would tend to imply a comparison between pinnules and entire leaves, a comparison which cannot be sustained on morphological grounds. If Asama's principle of fusion and reduction is applied, there should be vestiges of scaled down, fused pinnules in the entire leaves found in the Hazro area. These do not occur. The Hazro specimens are sufficiently complete to dismiss the notion that large pinnules rather than entire leaves might be represented.

The original collection from Hazro was made in a single afternoon and in view of the considerable variety of plant remains obtained on that occasion, it seemed useful to return to the locality and to gather a larger collection. This aim was finally realized in 1979 and 1980 when R. H. Wagner had the opportunity to study the stratigraphical succession in the Hazro inlier, at about 70 km ENE of the provincial capital Diyarbakır, and to collect new material including several specimens of the disputed species of *Glossopteris*. A short list with partly revised identifications was given in Fontaine *et al.* (1980) and a paper providing stratigraphical details is being prepared in collaboration with E. Demirtaşlı of the Mineral Research and Exploration Institute of Turkey. The present paper is the first contribution to a full description of the floral elements collected from the Upper Permian rocks at Hazro. Foraminiferal data reported by Fontaine *et al.* (1980) have allowed dating the plant-bearing succession as Dzhulfian, i.e. the highest Permian.

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Acknowledgements

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The Royal Society of London and CONICET in Buenos Aires made it possible for S. Archangelsky to study the material from Hazro in the University of Sheffield, and to compare it with other species of *Glossopteris* in the collections of the British Museum (Natural History) and of the Sedgwick Museum in Cambridge, to which Dr C. R. Hill and Dr N. F. Hughes kindly granted access. Facilities at the Geology Department, University of Sheffield, are also gratefully acknowledged, and Howard Crossley is thanked for photographic assistance. The BM(NH) made a photograph available of the type specimen of *Glossopteris stricta* Bunbury which is reproduced here.

Systematic description

Order **GLOSSOPTERIDALES**

Genus ***GLOSSOPTERIS*** Brongniart 1822

Glossopteris anatolica sp. nov.

Figs 1–8, 11, 13–14

1959 *Glossopteris stricta* Bunbury; Wagner: 1379–1381 (*non* Bunbury 1861: 331; pl. IX, fig. 5).
1962 *Glossopteris* cf. *stricta* Bunbury; Wagner: 745–746; pl. 24, figs 2, 2a (part), fig. 3; pl. 25, fig. 5 (part), figs 6, 7, fig. 8 (part).
1980 *Glossopteris* sp. nov.; Wagner *in* Fontaine *et al.*: 919.

Diagnosis. Leaves extremely variable in size, the longest (incomplete) fragment measuring 10 cm × 3·4 cm at constant width (this specimen lacks both base and apex). Midrib strong, up to 4 mm wide, and consisting of several parallel strands; it persists into the leaf apex. Base of leaf acute, probably cuneate; apex obtuse (*c.* 90°), slightly emarginate in smaller specimens. Lateral veins decurrent, strongly arching near midrib and passing to the leaf margins at angles of 65° to 80°, which become slightly less in the apical part (*c.* 50°). Anastomoses and somewhat less common pseudo-anastomoses form a compact mesh with short areolae near the midrib (1·5–2 mm long and 1 mm wide) and passing into more elongate, narrower meshes towards the margins and in the apical part of the leaf.

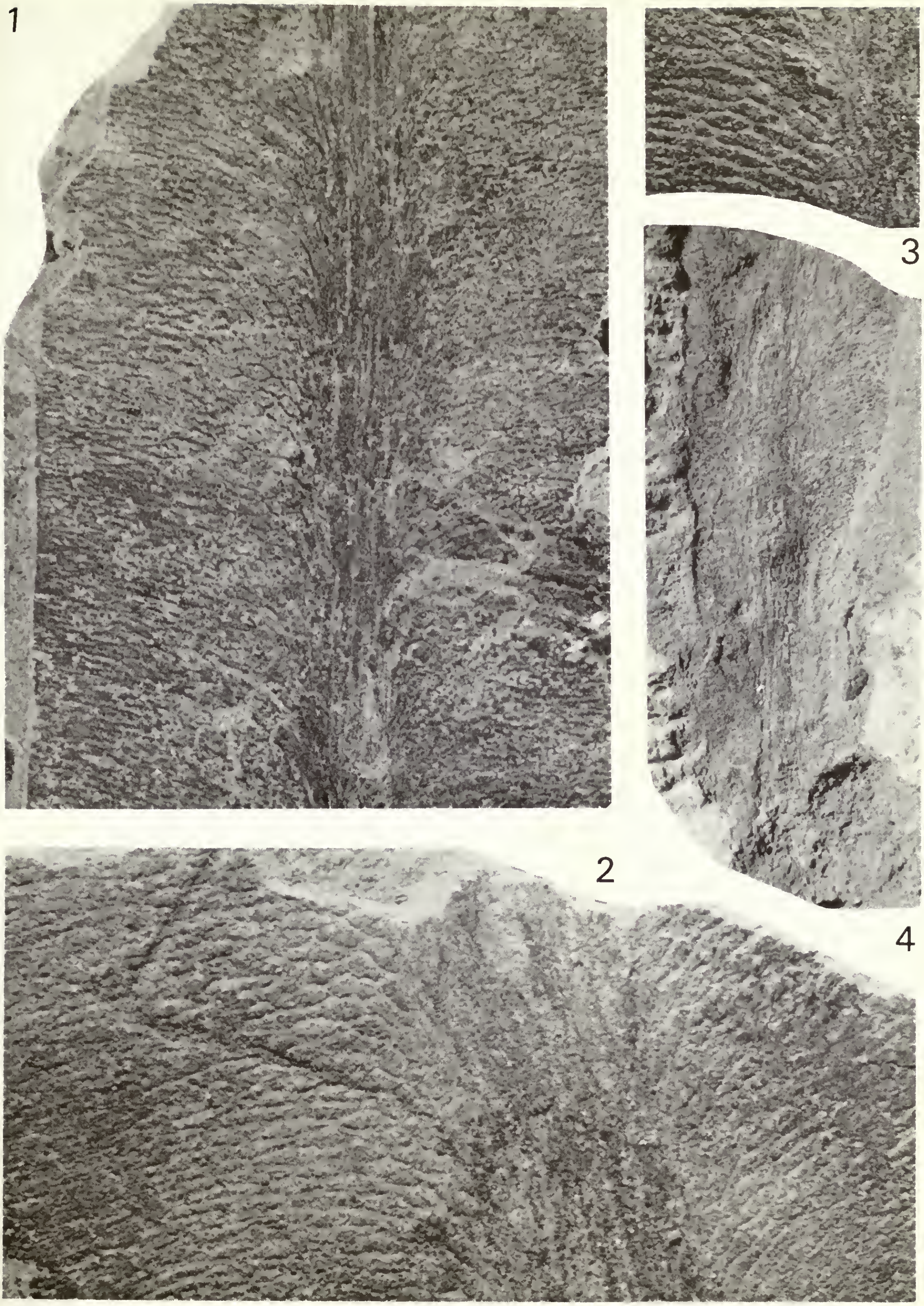
Holotype. British Museum (Natural History) register no. V.60797.

Paratypes. BM(NH) V.60793–6 and V.60798–801, and additional specimens from the type locality (Wagner loc. no. 3111) in the Natural History Museum of Maden Tetkik ve Arama Enstitüsü, Ankara.

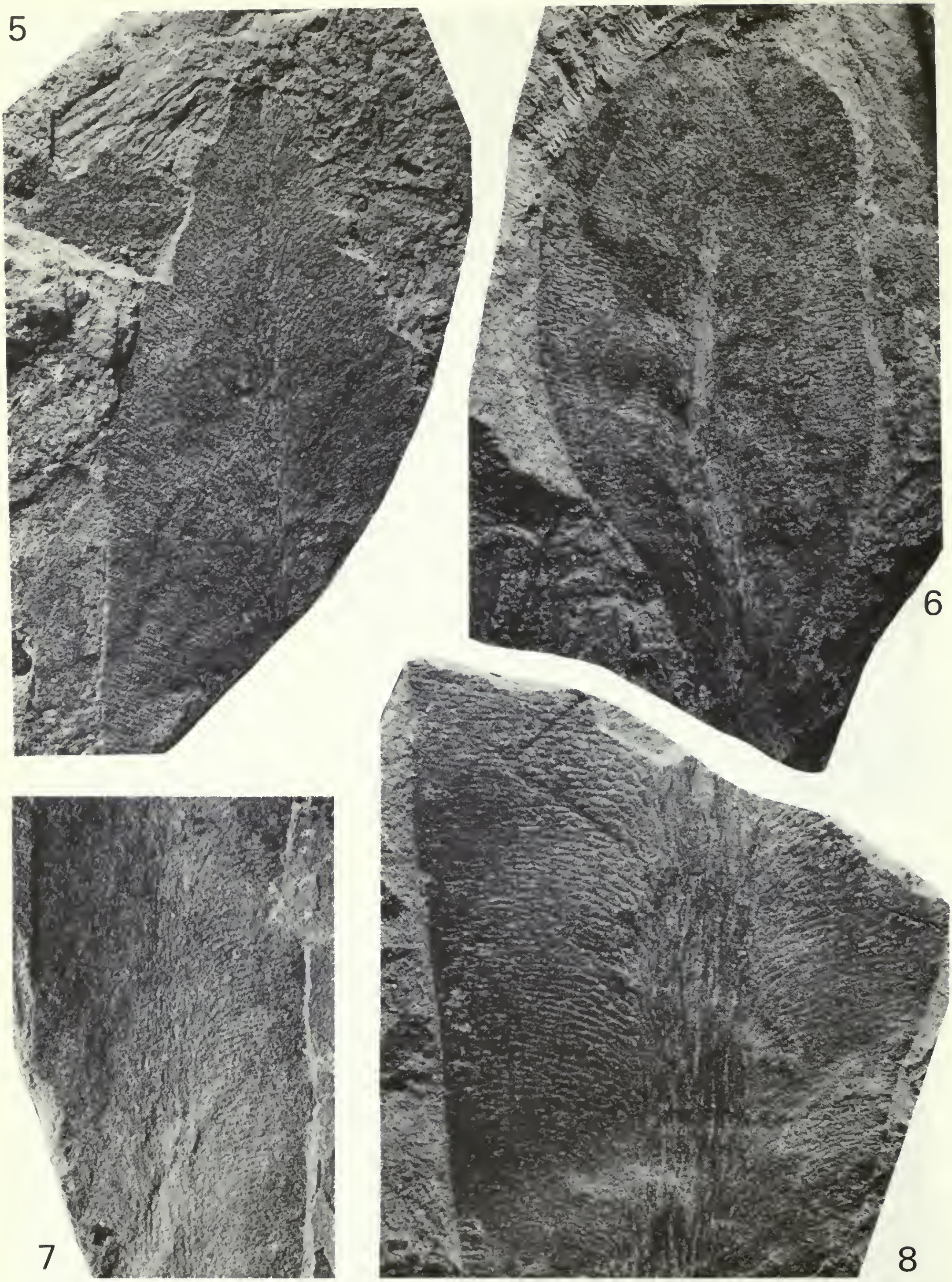
Type locality. Coal-bearing succession of the Gomaniimbrik Formation exposed at 750 m SSW of Dadaş village in the western part of the Hazro inlier, *c.* 70 km ENE of Diyarbakır in south-east Anatolia, Turkey.

Name. Anatolia, the Asian part of Turkey.

Description. The specimens figured in 1962 are joined by new collections made from different bands in the same general locality south of Dadaş in the western part of the Hazro inlier. Unfortunately, no complete leaves have been obtained, the most entire specimen (Fig. 6) being a rather small leaf, 4 cm long and 1·8 cm wide in the middle. It shows an obtuse, slightly emarginate apex. Larger specimens are up to 10 cm long (Fig. 1), despite the lack of preserved bases and apices. It is assumed that these leaves reached an approximate length of 15 cm or more. Their observed maximum width is 4 cm, and it thus appears that the larger leaves may have been narrowly oblong, lorate (following the terminology established by Dilcher, 1974, and



Figs 1–4 *Glossopteris anatolica* sp. nov. Fig. 1, middle part of a leaf showing a wide midrib and the characteristic lateral vein meshes, BM(NH) V.60793, ×3. Figs 2–3, middle part of leaf with characteristic venation, BM(NH) V.60794, ×6. See also Fig. 8. Fig. 4, basal part of a leaf, BM(NH) V.60795, ×3.



Figs 5–8 *Glossopteris anatolica* sp. nov. Fig. 5, apical part of a leaf, BM(NH) V.60796, ×3. Fig. 6, small leaf showing the base as well as a slightly emarginate apex, **Holotype** BM(NH) V.60797, ×3. Fig. 7, part of a small, narrow leaf, BM(NH) V.60798, ×3. Fig. 8, middle to near-basal part of leaf with a strong midrib and characteristic lateral veining pattern, BM(NH) V.60794, ×3. (Details of the same specimen, ×6, see Figs 2–3).

adopted for *Glossopteris* leaves by Chandra & Surange, 1979). Apical and near-basal leaf fragments were illustrated in 1962, and also appear in the new collections (Figs 4, 5).

The midrib is strong, always persistent to the apex, and rather wide in the basal part of the leaves. It consists of several (usually 5 to 6) parallel, non-anastomosing strands (Fig. 14). Lateral veins are decurrent in the basal and medial sectors of the leaves, and slightly less decurrent near the apex. They are strongly arching quite near the midrib (Figs 2, 7, 8, 11), i.e. within a distance of 4 to 5 mm, and run a straight, subparallel course in most of the width of the leaves, reaching the leaf margin generally at angles of 65° to 75° (overall variation is 50° to 80°). The vein pattern is reticulate throughout, with an apparent predominance of complete anastomoses, but also showing pseudo-anastomoses. The arching veins near the midrib show a mesh with short and wide areolae; more elongate, narrower vein meshes occur in the straighter, subparallel course of the veins towards the leaf margin (Figs 3, 13).

COMPARISONS. The most comparable species is *Glossopteris stricta* Bunbury, as described from the Upper Permian Kamthi 'Stage' of India (Bunbury 1861, Chandra & Surange 1979). The Anatolian species differs mainly in the secondary venation. Although the general pattern of vein meshes is similar, with short and broad areolae near the midrib and narrower, more elongate meshes towards the margin, it is noted that the veins of *G. stricta* are not quite as decurrent as in *G. anatolica*. They also meet the leaf margin at almost 90°, whereas the angle varies between 50° and 80° in *G. anatolica* (depending on the size of the leaf and the position of the veins within the leaf). Also, the apex of *G. stricta* leaves is more acute and does not display the emargination seen in at least one specimen of *G. anatolica* (Fig. 6). Although the general shape of the leaves appears to be similar in both species, it seems that the leaves of *G. stricta* are relatively longer (as follows from an examination of the lectotype, BM(NH) V.19620, which shows a length/breadth ratio of about 10:1). Making allowance for the incompleteness of the known leaves of *G. anatolica*, it appears that these show a length/breadth ratio of up to 6:1. The lectotype of *Glossopteris stricta* Bunbury has been refigured by Banerjee (1978: pl. 8, figs 17–18).

Glossopteris leaves described as *G. stricta* from Patagonia in South America (Archangelsky 1958a, b) are comparable to *G. anatolica* in the general shape, size and anastomosed vein pattern. However, the Patagonian leaves are different in having longer and narrower vein meshes near the midrib, and possessing less decurrent lateral veins. Complete specimens from Patagonia display a length/breadth ratio of 9:1, as against a probable 6:1 ratio for *G. anatolica*.

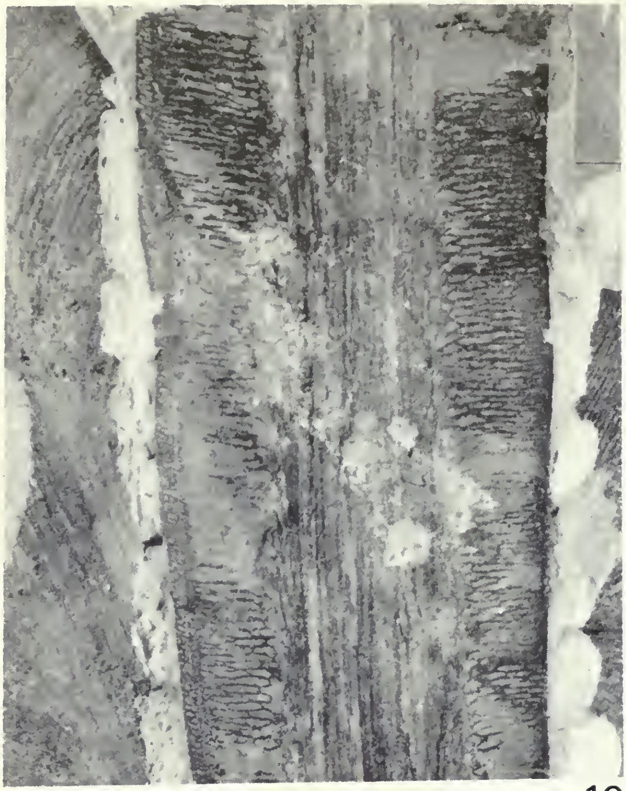
Glossopteris stricta Bunbury, as recorded from Antarctica by Plumstead (1962), shows somewhat less decurrent lateral veins which display a tendency towards free veining near the leaf margin (compare Plumstead 1962: pl. X, fig. 1; pl. XI, fig. 1).

Glossopteris indica Schimper, as revised by Chandra & Surange (1979), is a polymorphic species, with a changing length/breadth ratio as the species is followed up the stratigraphic column. Ratios of 6:1, 4:1 and 3:1 are recorded for the Barakar, Kamthi and Raniganj 'stages' in upward succession. The lateral veins of *G. indica* are not decurrent near the midrib, and they usually abut onto the leaf margin at angles of *c.* 45° to 50°, reaching angles of up to 70° in some medial portions. *G. anatolica* shows clearly decurrent veins near the midrib in the basal, medial and apical parts of leaves of all sizes. It is also noted that the apex in *G. indica* is more acute than it is in *G. anatolica*. Also it never appears to be emarginate.

Glossopteris pantii Chandra & Surange (1979) is a leaf of similar shape to that of *G. anatolica*, albeit with an obtuse-cuneate base as against an acute-cuneate base in the latter. Moreover, its veins follow a different pattern, being more horizontal in the medial sector and reaching the leaf margin at 45° in the basal parts of leaves. This contrasts with the venation of *G. anatolica* which is more generally uniform in different parts of the leaf. Also, the areolae near the midrib are shorter and wider in *G. anatolica*, which displays a more marked contrast in mesh size and shape between the central and marginal parts of the leaf.

Glossopteris arberi Srivastava (1956) shows leaves of similar size and shape to those of *G. anatolica*, but its lateral veins dichotomize only 2–3 times and the areolae are correspondingly longer than those of the Anatolian species.

Glossopteris tortuosa Zeiller, as figured by Plumstead (1952: pl. 49, fig. 4) from South Africa,



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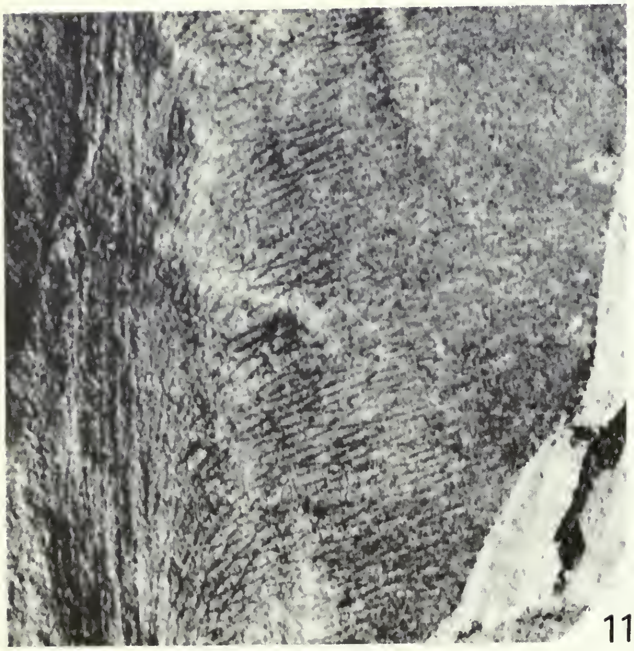

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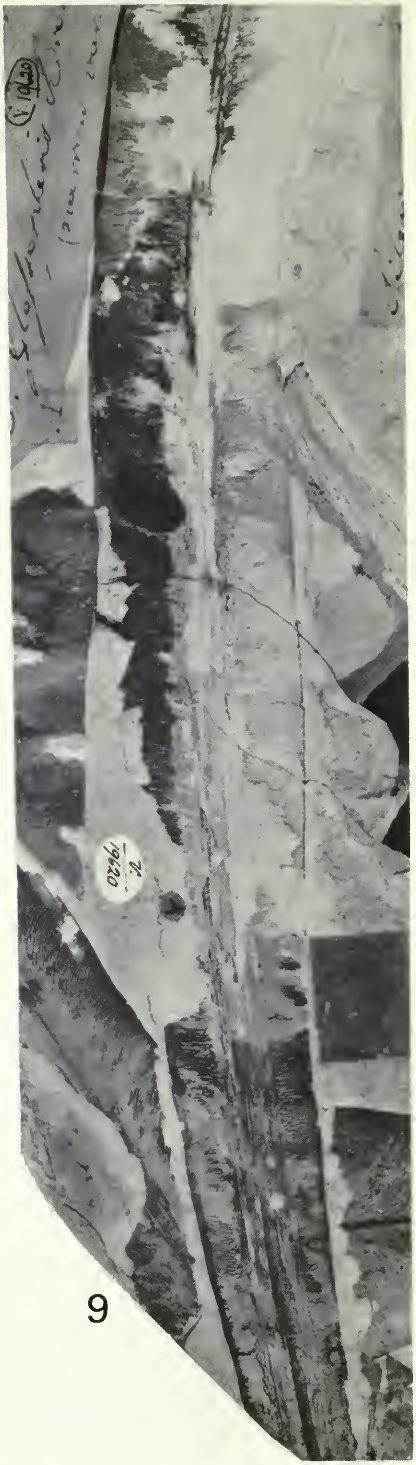

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Figs 9–10 *Glossopteris stricta* Bunbury. Fig. 9, lectotype (Bunbury 1861: pl. 9, fig. 5), BM(NH) V.19620, ×1. Fig. 10, detail of the venation of the lectotype (lower part of the leaf), ×3.
Fig. 11 *Glossopteris anatolica* sp. nov. Detail of the lateral vein meshes (for comparison with *G. stricta*), BM(NH) V.60799, ×3.

differs from *G. anatolica* in the shape of its leaves which are broadly ovate. It also shows narrower vein meshes near the midrib than occur in the latter.

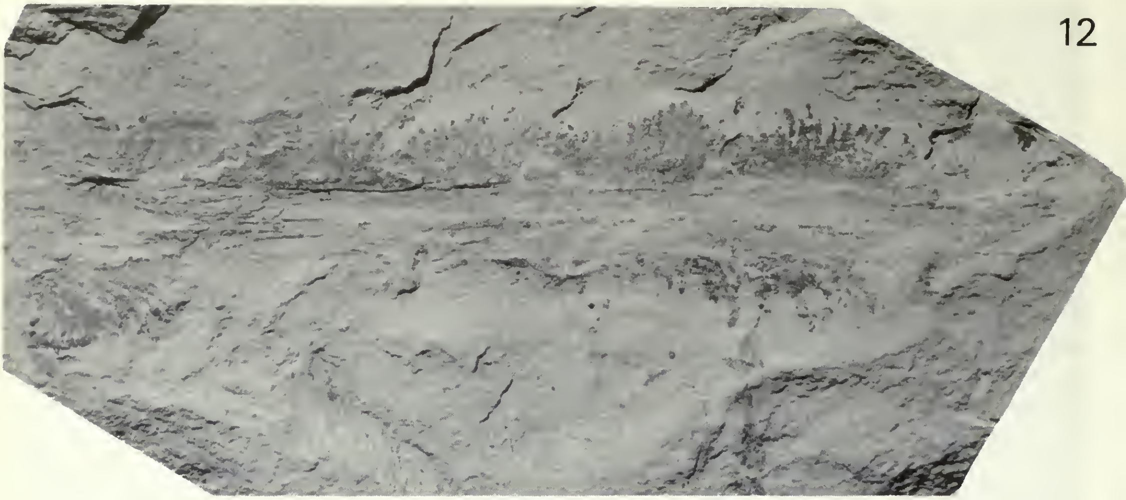
Discussion. *Glossopteris* leaves have been found in three different bands in the Gomaniimbrik Formation south of Dadaş village in the Hazro inlier. They are common without being abundant, about 30 specimens having been found altogether. Every single specimen shows the characteristic nervation of *Glossopteris anatolica*, and it is clear that only a single species is represented. No cuticle has been recovered from any of these specimens and there are no fructifications assignable to *Glossopteris* associated with the leaf prints (Professor W. S. Lacey, who kindly examined some poorly-preserved fructifications from the original collection from Hazro, did not find convincing evidence of any *Glossopteris* fructification, although some specimens seemed to suggest the possibility – Lacey, *in litt.* 30.XI.62). On the other hand, the midrib composed of parallel strands and the characteristic mesh formed by anastomosed and pseudo-anastomosed lateral veins do not admit of a generic attribution other than to *Glossopteris*. The comparisons made with several undisputed *Glossopteris* species emphasize this point.

The Hazro flora

It remains to explain the presence of *Glossopteris* in an assemblage of plants which are mainly characteristic of the equatorial belt and not of the Gondwana Realm. A revision of the floral remains recorded in 1962 from Hazro, in conjunction with the new material collected from different bands in the same locality, has been undertaken by R.H.W. A revised list of taxa, incorporating additional species discovered most recently, is as follows: *Glossopteris anatolica* Archangelsky & Wagner sp. nov., *Bicoemplectopteris hallei* Asama, *Taeniopteris* sp., *Botrychiopsis* sp., *Fascipteris hallei* (Kawasaki) Gu & Zhi, *Pseudomariopteris hallei* (Stockmans & Mathieu) Wagner, *Cladophlebis tenuicostata* (Halle) comb. nov., *Sphenopteris* sp., *Pecopteris* (*Asterotheca*?) *calcarata* Gu & Zhi, *Dizeugotheca*? sp. nov., *Pecopteris nitida* Wagner, *Pecopteris pirae* Wagner, *Sphenophyllum* cf. *koboense* Kobatake, *Lobatannularia heianensis* (Kodaira) Kawasaki, *Cordaites* sp.

This is not the place for a full discussion of the revision which is still in progress. However, a few brief comments may be in order. *Bicoemplectopteris hallei* refers to the specimens figured as *Gigantopteris nicotianaefolia* in 1962 (see Asama, 1976: pl. XXX, fig. 6). *Fascipteris hallei* is the material recorded as '*Validopteris*' sensu Stockmans & Mathieu (*non* Bertrand) in 1962. *Cladophlebis tenuicostata* has been identified mainly from new material, but incorporates specimens recorded originally (Wagner 1962) as *Pecopteris tenuicostata* Halle and *Cladophlebis roylei* Arber. The new combination is based on *Pecopteris tenuicostata* Halle as figured and described from the Upper Shihhotse of central Shansi, China (Halle 1927: 99–100; pl. 26, figs 1–2). *Pseudomariopteris hallei*, *Sphenopteris* sp. and *Pecopteris calcarata* are new identifications based on specimens collected most recently. *Dizeugotheca*? sp. refers to a fertile pecopterid similar to that figured from Saudi Arabia by El-Khayal *et al.* (1980: fig. 2c). Sterile remains of this plant were illustrated in 1962 under the name of *Pecopteris* cf. *wongi* Halle pars (see also Lemoigne 1981: pl. 6, fig. 1). *Pecopteris nitida* Wagner, which is now available in large specimens showing the variation within the frond, also incorporates the remains identified in 1962 as *Pecopteris phegopteroides* (Feistmantel) and *Pecopteris jongmansi* Wagner. Recent investigations on the Permian flora of Unayzah in Saudi Arabia, undertaken by R.H.W. in collaboration with Dr A.A. El-Khayal of King Saud University, Riyadh, have shown that *Pecopteris tenuidermis* Wagner (1962) represents the cuticular imprints of pinnules of *Pecopteris pirae* Wagner. The single leaves of *Zamiopteris*? sp. figured in 1962 proved to belong to *Sphenophyllum* cf. *koboense* Kobatake, a Late Permian species in which the leaves show the development of a midvein.

Wagner (1962) claimed that the Hazro flora contained a mixture of Cathaysian and Gondwana elements. The Cathaysian aspect of this flora has not been seriously disputed, and the newly discovered additional species have strengthened the comparisons with the East Asian



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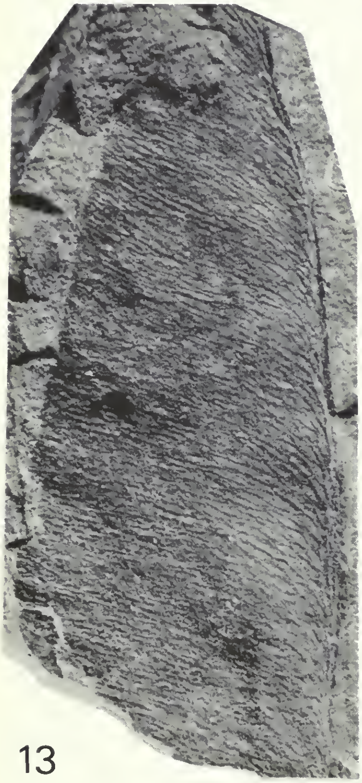

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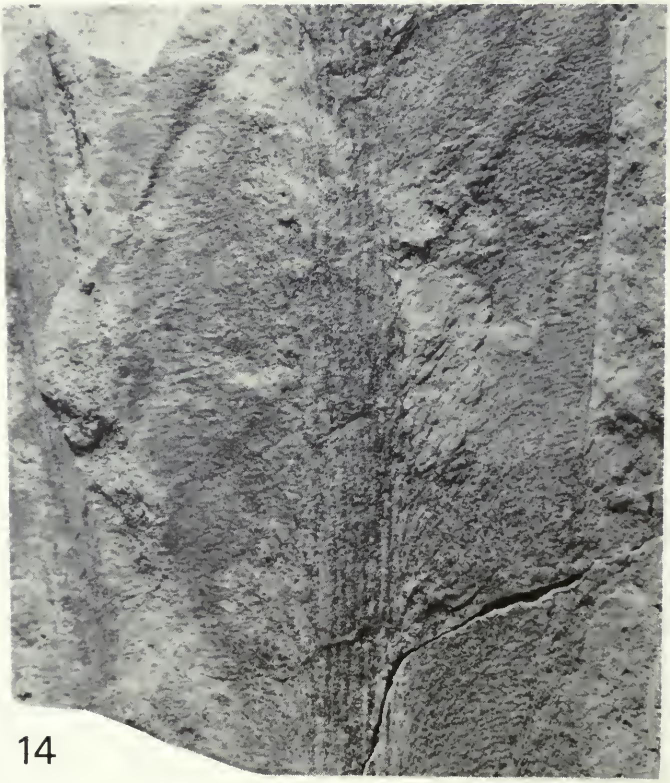

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Fig. 12 *Botrychiopsis* sp. Basal portion of a frond showing a double row of pinnules, with totally fused lamina at the extreme base and more individualized, semicircular pinnules a little higher up. BM(NH) V.60802, ×3. Part of this specimen was figured by Wagner (1962: pl. 26, fig. 12).

Figs 13–14 *Glossopteris anatolica* sp. nov. Fig. 13, detail of lateral veins in the apical sector of a leaf, BM(NH) V.60800, ×3. Fig. 14, lower part of a leaf showing the wide, striate midrib formed by parallel strands, BM(NH) V.60801, ×3.

Cathaysia flora. The Gondwana component has been regarded as more controversial. *Glossopteris anatolica* is the most striking representative of the Gondwana flora at Hazro where it is of common occurrence. Its Late Permian (Dzhulfian) age puts it near the end of the stratigraphical occurrence of the genus, and this implies that the Anatolian species had sufficient time to migrate from the main area of the Gondwana Realm where *Glossopteris* is both diversified and abundant. The palaeogeographic position of India alongside East Africa and Madagascar provides the possibility of a direct migration route from either India or eastern Africa. The upper Mesopotamian region, to which Hazro belongs, can be regarded as the northernmost part of the Arabian Shield which forms part of the Gondwana Plate.

Another plant of Gondwana affinity in the Hazro flora is that figured as *Dicroidium*? vel *Thinnfeldia*? sp. by Wagner (1962: pl. 26, figs 12–13). Lacey (in Discussion of Wagner 1962) compared these specimens with the basal parts of the frond of *Neuropteridium validum* Feistmantel. He later referred to them as cf. *Gondwanidium validum* (Feistmantel) Gothan (Lacey 1975: 129) and quoted Archangelsky (1971, personal communication) as supporting this identification. Only two specimens are available from the old collection and no further remains have come to light. The most complete specimen is refigured here as Fig. 12. It was only partially figured in 1962. This specimen shows a wide rachis with fine longitudinal striations, and two lateral laminae with little differentiation in the basal part and gradually more individualized pinnules higher up. The venation of the individual pinnules is decurrent, dichotomous, and generally odontopteroid. The pinnules are broadly attached, and almost semicircular, being about twice as wide as they are high. There is a reasonable resemblance to the basal parts of fronds of *Botrychiopsis* (= *Gondwanidium*) as figured by Archangelsky & Arrondo (1971: pl. I). Three species of *Botrychiopsis* are known at present: *B. weissiana* Kurtz, *B. plantiana* (Carruthers) Archangelsky & Arrondo, and *B. valida* (Feistmantel) Archangelsky & Arrondo. The specimens from Hazro cannot be identified with any of these. Furthermore the Hazro flora is very Late Permian in age whilst the youngest of these species, *Botrychiopsis valida*, belongs to the Early Permian (for a recent description, see Archangelsky & Cúneo, 1981). Although it may be assumed that the Hazro specimens belong to a new species of *Botrychiopsis*, the material is inadequate for a proper description, particularly in view of the fact that *Botrychiopsis* fronds show a good deal of variation as a result of lobing. This variation can be brought out only by large specimens or many different fragments from a single locality. Since most of the Hazro flora is of Cathaysian affinity, a sustained search was made in the literature for any comparable species from the contemporaneous equatorial belt. This failed to produce results. The Hazro specimens are therefore assigned confidently to *Botrychiopsis* sp., and it is assumed that this is another immigrant from the Gondwana Realm.

Two other species mentioned in 1962 were also assumed to be indicative of a Gondwana affinity. One of these, *Pecopteris phegopteroides* (O. Feistmantel) (Wagner 1962: pl. 25, fig. 8 *pars*; pl. 28, fig. 26 – with cf.), cannot be retained in the list of species from Hazro. Fairly large fragments of the frond of *Pecopteris nitida* Wagner, which have been collected most recently, have shown that the specimens figured as *P. phegopteroides* fall within the range of variation of the latter species. The second putative Gondwana element, *Cladophlebis roylei* Arber (Wagner 1962: pl. 27, figs 16–17), is here referred to *Cladophlebis tenuicostata* (Halle) comb. nov. Additional material from the Hazro flora has shown a range of variation which apparently fits Halle's species from the East Asian Cathaysia flora. It is noted that *Cladophlebis mongolica* Durante, from the Permian of Mongolia, also seems to fit this species which Halle assigned to *Pecopteris*. Permian representatives of *Cladophlebis* are generally uncommon. They appear to be restricted to Upper Permian strata and it is assumed here that they are elements of the warm, humid, equatorial belt floras, which are found only occasionally in Upper Permian Gondwana assemblages.

General considerations on floral distribution

Wagner (1962) presented a map on which the Hazro locality was shown as belonging to both the Cathaysian (of the palaeoequatorial belt) and Gondwana realms. Chaloner & Lacey (1973) and

El-Khayal, Chaloner & Hill (1980) modified the northern boundary of the Gondwana Realm, leaving the Hazro locality well inside the palaeoequatorial belt. This is consistent with the information obtained most recently, which strongly emphasizes the Cathaysian connection. Also, the Saudi Arabian flora reported by El-Khayal *et al.* (1980), and which is currently being investigated in more detail, shows clear Cathaysian affinities. This flora is at present regarded as being of mid-Permian age. Lemoigne (1981) even referred to it as belonging to the Upper Permian. The boundary between palaeoequatorial (*sensu lato*) and Gondwana floras shown on the map published by El-Khayal *et al.* (1980), and which we accept as more nearly correct in the light of current information, leaves most of the Arabian Peninsula in the palaeoequatorial belt. The lack of information from southern Arabia and the horn of Africa makes it also possible that the northern boundary of the Gondwana Realm should be even further south, leaving the entire Arabian Shield in the palaeoequatorial belt (compare Lemoigne, 1981). Most palaeogeographic reconstructions place India alongside eastern Africa. These two areas are here regarded as the likely source for the two plants of Gondwana affinity in the Hazro flora, i.e. *Glossopteris anatolica* and *Botrychiopsis* sp. It is a well-known fact that Permian times saw an appreciable amelioration of climate which led to substantial mixing of floral elements. This is mainly recorded as the influx of 'equatorial', presumably more thermophile, elements into the Gondwana floras which thus became a little less restricted in composition. The reverse migration, from the Gondwana Realm into the equatorial belt, is less well documented, and it seems that the Hazro flora provides one of the rare examples of it. It is probably no coincidence that this migration is found in a flora of the latest Permian age. *Glossopteris* is almost exclusively a Gondwana element which lived in a temperate climate. The migration of *Glossopteris anatolica* to lower latitudes, and a warmer climate, may have been aided by the fact that the Hazro locality coincides with the northern edge of the Gondwana Plate in upper Mesopotamia. There seems to have been a continuous land area from East Africa/India to Arabia and Mesopotamia.

Another, more spectacular case of migration of the glossopterids is recorded by Zimina (1967, 1977), who figured and described three species of *Gangamopteris*, two of *Glossopteris* and one of *Palaeovittaria* from the region of Vladivostok in the Soviet Far East. These occur in the lower part of the Upper Permian.

'Gu & Zhi' (1974: pl. 110, figs 3–4) recorded a *Glossopteris guizhouensis* from the lower part of the Upper Permian in Guizhou (Kuichow) Province in China, but this species has recently been transferred to a new genus, *Abrotopteris*, which may be unrelated to the glossopterids. This species is currently described as *Abrotopteris guizhouensis* (Gu & Zhi) Mo (Zhao Xiuhu, personal communication).

Attention is drawn to Kon'no's (1963) record of *Glossopteris* cf. *angustifolia* Brongniart from the Permian deposits of Phetchabun in Thailand. Asama (1966), who studied the Phetchabun flora in more detail, accepted Kon'no's record in principle but mentioned that the specimen figured by Kon'no had an indistinct venation and that further collecting from the Phetchabun locality failed to turn up additional remains. In fact, he hinted at the possibility that the specimen might belong to *Taeniopteris*. The Phetchabun flora is in the East Asian Cathaysia Province.

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The crocodilian *Theriosuchus* Owen, 1879 in the Wealden of England

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Synopsis

A skull fragment from the Wealden of Brook (Isle of Wight) is described and referred to the genus *Theriosuchus* Owen, 1879, previously known from the Purbeck of England. A little-known previous report of *Theriosuchus* teeth from the Wealden is discussed. Isolated procoelous vertebrae from the English Wealden named *Heterosuchus valdensis* by Seeley and often referred to the enigmatic crocodilian *Hylaeochampsa* may actually belong to *Theriosuchus*.

Introduction

This paper reports the previously overlooked occurrence of the crocodilian *Theriosuchus* in the Wealden of England. The genus *Theriosuchus* was erected by Owen in 1879, with *T. pusillus* as type species, for remains of a small crocodilian found by W. H. Beckles in the Purbeck Beds of Dorset. *Theriosuchus* may be a genus of great importance in crocodilian evolution. Its systematic position was interpreted variously before Joffe (1967) showed that it closely resembled the Atoposauridae from the Upper Jurassic of Europe, and suggested it should be included in that family. She also noted that *Theriosuchus* was very progressive in some respects (palatal structure, procoelous vertebrae) and might have been close to the ancestry of the Eusuchia, or have evolved in parallel with them. Although basically I agree with Joffe's conclusions, I think *Theriosuchus* may be sufficiently divergent from the typical Atoposauridae to warrant its inclusion in a separate family, as already suggested by Kälin in 1955 (see Buffetaut, 1982, for a more complete discussion).

The fossil reptile collection of the British Museum (Natural History) contains a fairly large number of remains of *Theriosuchus pusillus* from the 'Feather Bed' of the Middle Purbeck (see Joffe, 1967, for more details). However, apart from a very brief report, apparently overlooked by all later authors, which will be discussed below, there was until now no record of *Theriosuchus* from other localities.

In September 1980 Dr Peter Wellnhofer (Bayerische Staatssammlung für Paläontologie und historische Geologie, Munich) was examining the Hooley collection of pterosaurs from the Wealden of the Isle of Wight in the British Museum (Natural History). While doing so he came across the fragmentary posterior part of the skull of a small crocodilian (reg. no. R.176), and later he kindly mentioned this to me. Although very incomplete, the specimen turned out to be identifiable as *Theriosuchus*.

Previous report of *Theriosuchus* from the Wealden

At first it was thought that this skull fragment was the first find of *Theriosuchus* in the Wealden, but a careful search through the literature revealed that the genus had already been reported from this formation. In 1912 there appeared in *Nature* a very short anonymous news item on fossils recently presented to the British Museum (Natural History), which is quoted here in full:

> The Geological Department of the British Museum (Natural History) has also recently received a valuable gift of Wealden fossils from the Revs P. Teilhard and F. Pelletier, S.J., who made the collection during a four years' residence near Hastings. A large proportion of the specimens are small teeth from bone-beds

which had previously been very little examined, and among them is the unique mammalian tooth described under the name of *Dipriodon valdensis* by Dr Smith Woodward in 1911. There are numerous teeth of the dwarf crocodile *Theriosuchus*, which has hitherto been known only from the Purbeck beds. The series of plant-remains is also important and will shortly be described by Prof. A. C. Seward in a communication to the Geological Society.

In the discussion following the 1911 paper by Woodward on the above-mentioned mammal tooth, Charles Dawson had mentioned that Teilhard de Chardin and Pelletier (who were then studying theology at Hastings) had been helping him for two years in his researches on the Wealden bone beds of the Hastings area.

The report in *Nature* went unnoticed, and I have been unable to find any later mention of *Theriosuchus* in the Wealden. The isolated teeth in question are kept in the British Museum (Natural History) under the collective numbers R.4424–31 inclusive. They come mainly from the Wadhurst Clay and the Ashdown Clay of Fairlight West, although some were collected near Brede (both localities in the vicinity of Hastings). Similar teeth (R.3697) were presented even earlier, in 1909, by Charles Dawson.

Some of these teeth are not especially characteristic, being of the usual crocodilian type, conical and pointed; they cannot really be identified with any accuracy. Others are more distinctive, being laterally compressed, with a low, rather blunt crown, which is somewhat leaf-shaped in profile; these are very reminiscent of the posterior teeth of *Theriosuchus pusillus*. However, supplementary and more convincing evidence for the occurrence of *Theriosuchus* in the Wealden of England is provided by the present skull fragment.

The skull fragment R.176

The skull fragment found by Dr Wellnhofer in the Hooley collection (Fig. 1) comes from the Wealden of Brook (also spelt Brooke) on the southern coast of the Isle of Wight. A detailed description of the Wealden section at Brook Bay is given by Osborne White, who mentions

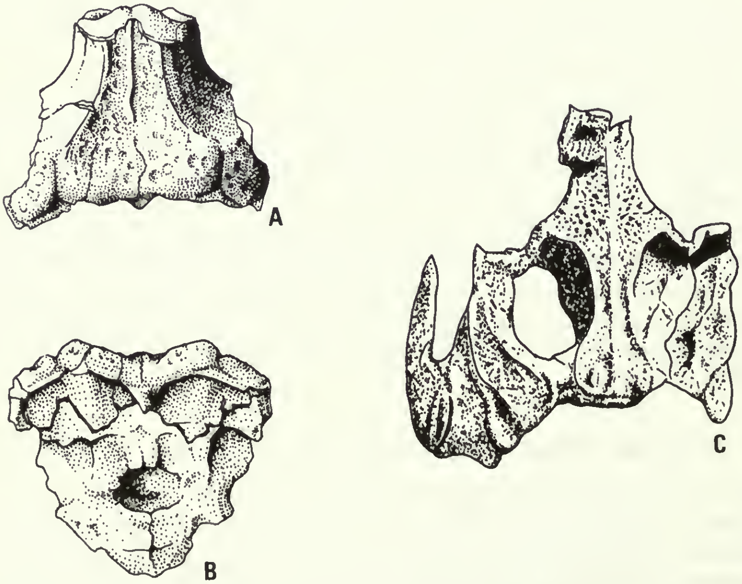

Fig. 1 A, B: Skull fragment of *Theriosuchus* sp. indet. from the Wealden of Brook, Isle of Wight, BM(NH) R.176, in dorsal (A) and posterior (B) views. C: posterior part of the skull of *Theriosuchus pusillus* from the Purbeck of Dorset, BM(NH) 48216, in dorsal view, for comparison (after Owen, 1879). All ×1. Drawings A and B by Dominique Visset.

(1921: 8) that 'the Wealden Beds of Brook Bay have yielded the remains of various large reptiles, including *Iguanodon bernissartensis* Boul., *Hoplosaurus hulkei* (Seeley), and *Heterosuchus valdensis* Seeley'. Incidentally, *Heterosuchus valdensis* is by no means a *large* reptile, but a small crocodilian, of which more will be said below.

The skull fragment comprises the greater part of the parietal, small medial portions of the squamosals, and parts of the bones of the occipital region (supraoccipital, exoccipitals, basioccipital); however, the occipital surface is poorly preserved, being much crushed and cracked. The lateral surfaces of the braincase are also very poorly preserved.

What is left of the parietal is roughly trapezoidal in outline, the bone becoming increasingly wider towards the rear. It is definitely narrower (7 mm) between the upper temporal fenestrae than farther posteriorly (maximum width 22 mm). Anteriorly, the parietal is incomplete, but apparently not much is missing. The dorsal surface of the bone is distinctly concave transversely, especially in its posterior part, as can readily be seen in posterior view. The anterolateral edges of the parietal are raised into blunt ridges, which extend forwards and become narrower between the upper temporal fenestrae. The dorsal surface of the bone is ornamented with small irregular pits. An interesting feature is the presence of a very well marked, fairly sharp, median ridge, which extends along the entire length of the bone. Posteriorly, the parietal overhangs the occipital surface. On this surface, there is a prominent triangular median tuberosity or spine, which seems to be formed partly by the parietal and partly by the supraoccipital. Only the dorsal part of the latter bone is preserved; it shows a pair of depressions, one on either side of the above-mentioned spine. More ventrally, the bones are so crushed that little is discernible; the site of the foramen magnum is still visible, but the occipital condyle has disappeared. When the dorsal surface of the parietal is placed in a horizontal plane, the occipital surface is seen to be sloping forwards at an angle of about 60°, a condition more primitive than in modern crocodilians (in which the occipital plane is nearly vertical), but not so archaic as in many mesosuchians. The occipital surface seems to have been high relative to its width. As mentioned above, little is left of the squamosals. A remarkable feature is the presence of a fairly deep and very distinct groove between the parietal and the squamosals. The latter seem to have had relatively well developed posterior expansions; in dorsal view, the posterior edge of the skull roof is distinctly concave.

Although fragmentary, this specimen exhibits several features present in *Theriosuchus pusillus*, suggesting its reference to the same genus. The shape of the parietal is very similar, although its posterior part is wider in the Wealden specimen than in those from the Purbeck. The lateral ridges on the parietal also occur in *Theriosuchus pusillus*, and the sharp median ridge is a constant feature of all specimens from the Purbeck. The grooves between the parietal and the squamosals are present both in the fragment from Brook and in *Theriosuchus pusillus*. The ornamentation of the skull table of the Wealden specimen is very reminiscent of that of the Purbeck form. Comparison of the occipital surfaces is hardly possible, since that region, although not much flattened, is poorly preserved in the Wealden fossil, while all the Purbeck specimens are strongly compressed dorsoventrally.

The Wealden specimen is somewhat larger than the type of *Theriosuchus pusillus*, but it still indicates a small animal. Joffe (1967) suggested that most of the specimens of *Theriosuchus pusillus* were juveniles, but this seems doubtful. Her evidence was based partly on a single femur from the Purbeck referred to *Theriosuchus pusillus*, larger than other femora of the species. However, the femur can hardly be called a very diagnostic bone in crocodilians, and the specimen in question may not belong to *Theriosuchus*. The allegedly juvenile characters of the skull of *Theriosuchus pusillus* listed by Joffe are observable also in the Atoposauridae from continental Europe, which, according to Wellnhofer (1971), are not juveniles. It should also be mentioned that the crocodilian obviously related to *Theriosuchus* briefly described (but not yet named) by Langston (1974) from the 'Comanchean' (Lower Cretaceous) of Texas is hardly larger than the type of *Theriosuchus pusillus*. The Wealden specimen described here also suggests that *Theriosuchus* and its allies may never have grown to a large size.

The resemblances to *Theriosuchus pusillus* listed above indicate that the skull fragment from the Wealden of Brook should be referred to the genus *Theriosuchus*. However, the specimen is too incomplete to warrant a specific identification and I think it better to designate it as *Theriosuchus* sp. indet.

Stratigraphical range of *Theriosuchus*

The skull fragment from the Wealden of Brook provides the first really convincing evidence of the occurrence of *Theriosuchus* in the Lower Cretaceous of England, and thus extends its stratigraphical range, previously limited to the Purbeckian. This of course is only a small extension, since the Middle Purbeck beds which have yielded *Theriosuchus pusillus* are only slightly below the Jurassic–Cretaceous boundary as defined in Dorset by Casey (1963). According to Casey, the limit lies within the Purbeck beds, at the base of the 'Cinder Bed'. As shown by Joffe (1967), *Theriosuchus pusillus* comes from the 'Feather Bed', about 10 ft (3 m) below the 'Cinder Bed'. The time-span separating the Wealden *Theriosuchus* from the Late Jurassic *Theriosuchus pusillus* is certainly not very great.

The occurrence of *Theriosuchus* in the Wealden beds is not really unexpected, since the crocodilian faunas of the Purbeck and of the Wealden have several other elements in common (notably *Goniopholis crassidens* and *G. simus*, as well as the genus *Pholidosaurus*). *Theriosuchus* can now be added to the list of crocodilians known from the Wealden of England, which already includes the genera *Goniopholis, Pholidosaurus, Vectisuchus* (described by Buffetaut & Hutt, 1980) and *Bernissartia* (reported by Buffetaut & Ford, 1979).

Theriosuchus and *Heterosuchus*

Seeley (1887) described as *Heterosuchus valdensis* a series of procoelous vertebrae in a small nodule from the Hastings Sands of Hastings, which had been collected by Gideon Mantell and is now in the collections of the British Museum (Natural History) under reg. no. 36555. He also referred to this species 'a few isolated vertebrae of similar character' from the Wealden of Tilgate and of Brook, also collected by Mantell and later purchased by the British Museum. More isolated procoelous vertebrae from the Wealden were later referred to *Heterosuchus valdensis* by Lydekker (1888).

Lydekker (1887) suggested that the vertebrae named *Heterosuchus* by Seeley might actually belong to *Hylaeochampsa vectiana*, a peculiar crocodilian described by Owen (1874) from the Wealden of the Isle of Wight. *Hylaeochampsa vectiana* is known by a single incomplete skull, in which the internal nares are in a typical eusuchian position (i.e. totally enclosed by the pterygoids) and which shows a peculiar construction of the palate, with large openings in the ectopterygoids. The phylogenetic and systematic positions of *Hylaeochampsa* are still doubtful (Buffetaut 1975), as it is uncertain whether it is closely related to modern eusuchians or is the result of convergent evolution. Many authors have followed Lydekker's suggestion that *Heterosuchus* is probably a junior synonym of *Hylaeochampsa* (Kälin 1955, von Huene 1956, Romer 1956, 1966, Steel 1973). However, the skull of *Hylaeochampsa* was not associated with vertebrae, and the only reason to assume that the vertebrae of *Heterosuchus* belong with the skull of *Hylaeochampsa* is that in the Eusuchia skulls with internal nares in a position similar to that of *Hylaeochampsa* are associated with procoelous vertebrae like those of *Heterosuchus*. It should nevertheless be remembered that the evolution of a modern type of palate need not have been synchronous with that of procoelous vertebrae. This is beautifully shown by *Theriosuchus pusillus*, in which, as pointed out by Joffe (1967), there are already procoelous vertebrae, while the palate is still of advanced mesosuchian type. Similarly, the *Theriosuchus*-like crocodilian from Texas mentioned by Langston (1974) has an advanced mesosuchian palate and procoelous vertebrae. Since *Theriosuchus* is now known to occur in the Wealden of England, one may reasonably suppose that at least some of the procoelous vertebrae found in the same beds belong to that genus rather than to *Hylaeochampsa*. The latter may have had procoelous vertebrae, but this remains to be demonstrated by the discovery of associated skull and vertebral material.

Acknowledgements

I thank Dr Peter Wellnhofer for drawing my attention to the skull fragment described in this paper. I am also grateful to Dr A. J. Charig and to Mr C. A. Walker for making the *Theriosuchus* material kept in the British Museum (Natural History) available for study.

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A new conifer species from the Wealden beds of Féron–Glageon, France

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Synopsis

Cuticle studies of various Lower Cretaceous conifers revealed a plant with several unusual features, here described as *Brachyphyllum carpentieri* n. sp., known only from the Wealden beds of Féron–Glageon (Nord), France. Whilst resembling a typical *Brachyphyllum* Lindley & Hutton *ex* Brongniart species in gross morphology, the combination of lobed leaf margin, abaxial glands, minute hypodermal cells and a complex form of stomatal apparatus distinguish it from any other known conifer, fossil or extant. Silicified wood from the same locality has been described by Lemoigne & Demarcq (1967) and may belong to the same plant.

Introduction

During the recent revision of some Lower Cretaceous conifer species several hand specimens in the foreign Cretaceous collection at the British Museum (Natural History) were re-examined. More precisely the revision of a supposedly widespread conifer *Sphenolepis kurriana* (Dunker) Schenk (Fisher 1981) led to the examination of French material previously thought to belong to this species (Carpentier 1927, 1939). These French specimens from Féron–Glageon were given to the Museum by A. Carpentier in exchange for English Wealden specimens. Hand specimens of the French material bear a close resemblance to known German specimens of *Sphenolepis kurriana* (Dunker) Schenk. Several cuticle preparations were made using Schulze's solution for maceration. When examined microscopically it was immediately apparent that this conifer displays several unique features which clearly distinguish it from the other revised conifer species. The combination of a lobed leaf margin with glands opening into the notches between the lobes and a complex stomatal apparatus, coupled with extensive minute hypodermal cells which completely obscure the epidermis, could lead one to question whether the cuticle is indeed coniferous. However, the leaf shape, phyllotaxy and pattern of stomatal distribution could hardly be more typical of many *Brachyphyllum* species. It is interesting to note that Lemoigne & Demarcq (1967) raised a similar question concerning silicified wood described from the same locality. Evidence of association led them to suggest that the wood and the leafy shoots belonged to the same conifer although the wood had some characteristics which were not typically gymnospermous.

Systematic description

Order **CONIFERALES**

Form-genus ***BRACHYPHYLLUM*** Lindley & Hutton *ex* Brongniart

Brachyphyllum carpentieri sp. nov.

Figs 1–10

1927 *Sphenolepidium kurrianum* (Dunker); Carpentier: 71; pl. 19, figs 1–7.
1939 *Sphenolepidium kurrianum* (Dunker); Carpentier: 157; pl. 1, figs 1–11.

Diagnosis. Small shoots up to 3 mm wide. Leaves scale-like, tips free, arising from the centre of a rhomboidal leaf base cushion; leaf and basal cushion combined up to 3 mm long × 2 mm wide.

Free part of leaf up to one-third total length. Leaf margins converging at up to 55° towards bluntly pointed apex; margins microscopically lobed with glands present in notches between lobes.

(Adaxial cuticle imperfectly known). Abaxial cuticle up to 7 μm thick. Stomata occurring in two broad bands on leaf and basal cushion, concentrated on cushion, avoiding mid-line. Stomatal apparatus circular, guard cells deeply sunken below a ring of papillate, subsidiary cells; up to 6 papillae around rim of circular stomatal pit. Diameter of stomatal apparatus 28–44 μm ($n = 32$); stomatal orientation irregular. Ordinary epidermal cells rectangular or spindle-shaped, some bearing small papillae. Hypodermal cells small, oval to circular, strongly cutinized, randomly arranged in main part of leaf, diverging in lobes; 4–8 μm long × 3–5 μm wide ($n = 100$) with straight, unpitted anticlinal walls up to 1·5 μm wide.

HOLOTYPE. V.17064, British Museum (Natural History).

TYPE LOCALITY AND HORIZON. Féron–Glageon (Nord), France. Barremian.

MATERIAL. This species is common in the Wealden beds of Féron–Glageon, the precise locality of which was poorly understood until Lemoigne & Demarcq (1967) published the following details. The beds are near the Hirson–Avesnes railway line; 1 km west of Couplevoie (parish of Glageon) and barely 100 m from the boundary of the parish of Féron.

NAME. The species is named after Alfred Carpentier.

Description

The description is based on the holotype, V.17064, from the foreign Cretaceous collection in the British Museum (Natural History), Fig. 1, together with information from the work of

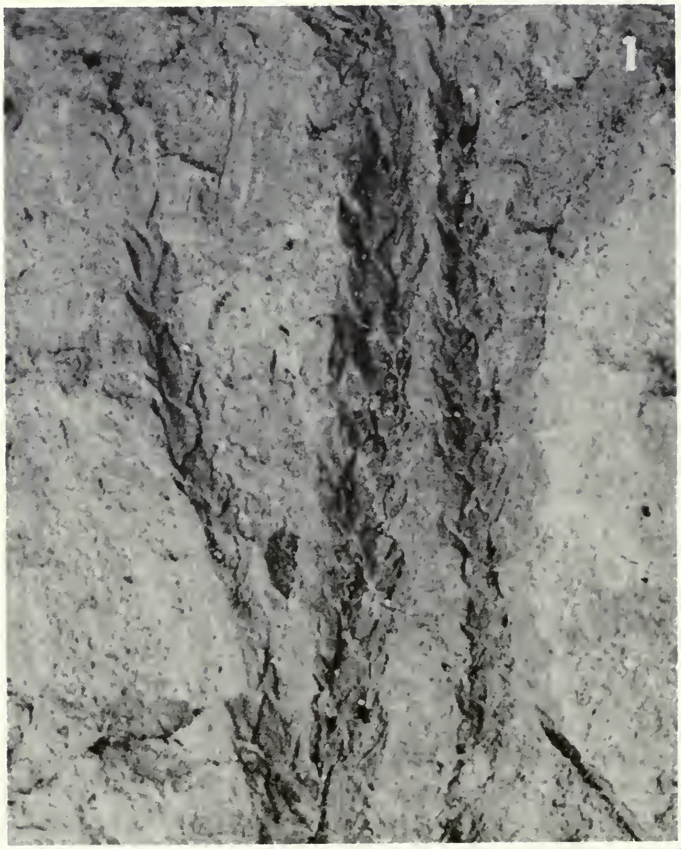
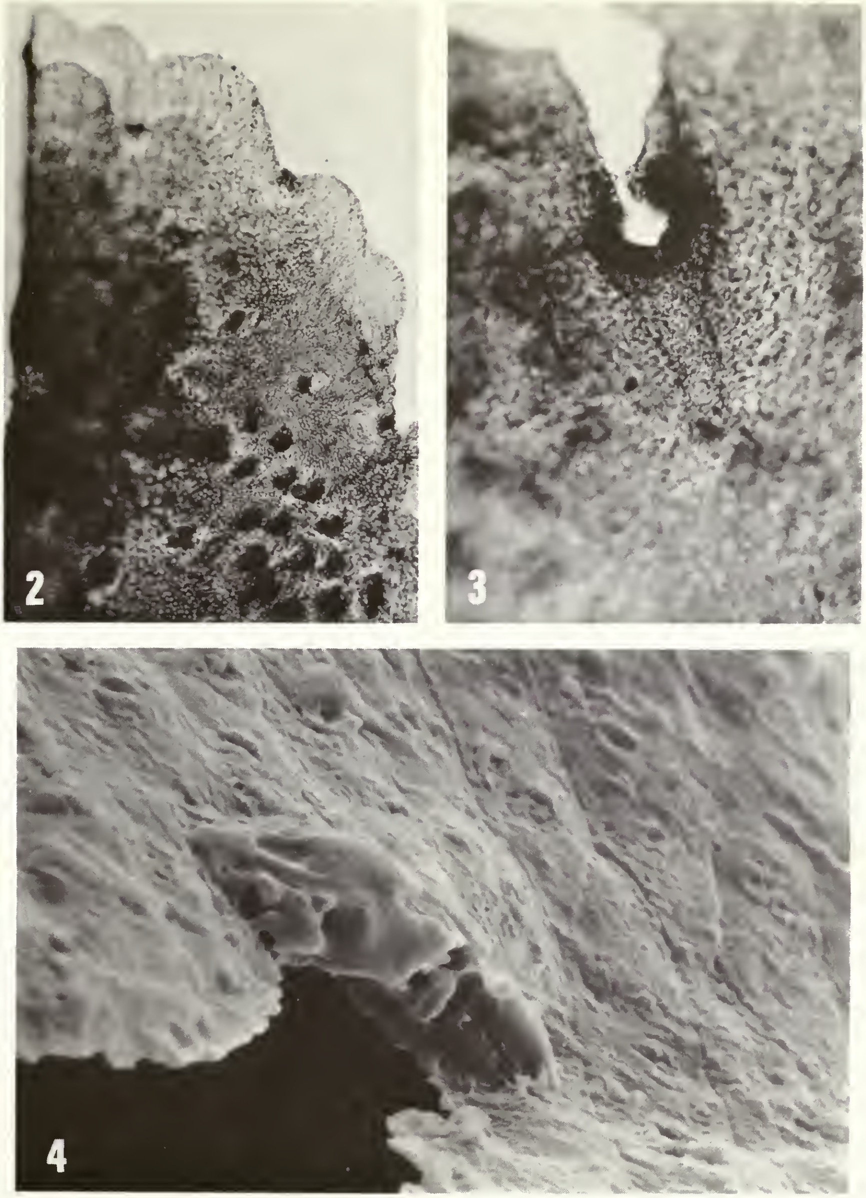
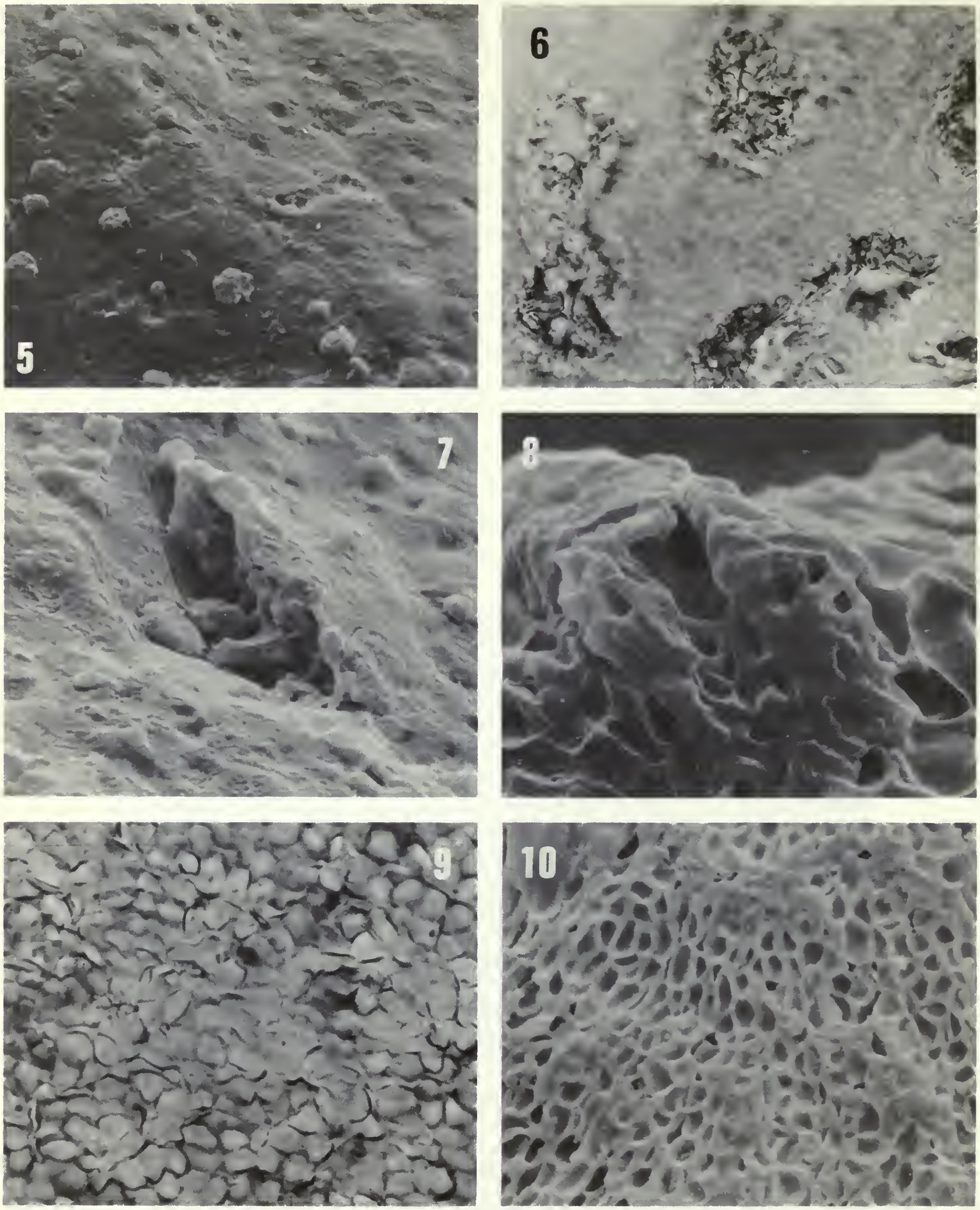


Fig. 1 *Brachyphyllum carpentieri* n. sp. **Holotype,** ×4. V.17064, BM(NH).



Figs 2–4 *Brachyphyllum carpentieri* n. sp. Fig.2, single leaf showing lobed margin; apex top left, patch of stomata bottom right, with unusual pattern of hypodermal cells between; ×100. Fig. 3, margin of leaf showing portions of two lobes with gland in notch between; ×175. Fig. 4, SEM view of portions of two marginal lobes in foreground with gland in notch between. Spindle-shaped epidermal cells with pitted walls show clearly on the right; ×700. All preparations from holotype, V.17064.

Carpentier (1927, 1939). Three of Carpentier's figures (1939: pl. 1, figs 1–3) agree with the cuticle obtained from the holotype in every detail. The remaining figures show the epidermal cells and subsidiary cells of the stomata; such detail has not been seen in cuticle preparations of the holotype. The small amount of cuticle remaining on V.17064 is thick and easy to prepare but most of the preparations are from the abaxial surface. Only a small part of the adaxial surface was seen, thus the stomatal distribution on the adaxial surface is still unknown.



Figs 5–10 *Brachyphyllum carpentieri* n. sp. Fig. 5, SEM view of outer surface showing papillae, pits and faint outlines of epidermal cells; ×700. Fig. 6, group of stomata showing subsidiary cell papillae around stomatal pits; ×400. Fig. 7, SEM view of outer surface showing probable stomatal pit; pits and papillae were as ill-defined as this in all SEM preparations. Epidermal cells just discernible; ×1000. Fig. 8, SEM view of inner surface of cuticle showing a stoma closely invested with highly cutinized hypodermal cells. Guard cells missing; ×2000. Fig. 9, hypodermal cells seen by light microscope; ×700. Fig. 10, hypodermal cells by SEM; ×700. All preparations from holotype, V.17064.

The epidermal details of the abaxial surface, though clearly seen in several of Carpentier's figures, are extremely difficult to distinguish in the preparations from the holotype because they are totally obscured by the tiny, thickly cutinized hypodermal cells. Under the light microscope ordinary epidermal cells are impossible to detect, but when the outside surface of the cuticle is viewed by scanning electron microscopy (SEM) the outlines of these cells are discernible (Figs 4, 5). They are long and rectangular or spindle-shaped, resembling those figured by Carpentier (1939: pl. 1, figs 4, 5). In these preparations of Carpentier, showing the epidermal cells clearly, there is no sign of hypodermal cells. Some epidermal cells bear papillae, often several per cell, but we can detect no pattern to the distribution of papillate cells. Many cells have pores or pits in the outer periclinal walls (Fig. 5), a feature exhibited by another Wealden conifer species (*Brachyphyllum obesum* Heer), which is to be redescribed in detail elsewhere.

In the greater part of the leaf and cushion the hypodermal cells are arranged in long arcs which radiate from the centre, swirl around the stomata and then diverge in the marginal lobes (Fig. 2). When the inside surface of the cuticle is viewed by SEM the nature of these hypodermal cells is fairly clear (Fig. 10). They are quite thickly cutinized, unpitted and very small, certainly the smallest of any conifer known to us.

The details of the stomatal apparatus are still imperfectly understood. Carpentier's figures (1939: pl. 1, figs 4, 6, 9, 10) show the stomatal apparatus to have 4–6 subsidiary cells with occasional encircling cells present. In V.17064 the hypodermal cells completely obscure the subsidiary cells (Fig. 6). Individual subsidiary cells have not been observed but using the light microscope up to six papillae have been seen around the stomatal pit. The stomata in Fig. 6 show those papillae quite clearly, yet by SEM the pits and papillae all appear ill-defined, as in Fig. 7. The guard cells are quite deeply sunken and have only been seen as rather eroded remnants.

The multicellular glands deeply embedded in the leaf tissue are another unusual feature. They frequently occur below many of the notches separating the marginal lobes and several are apparent in other parts of the leaf surface. The glands appear conical in shape with the widest part of the cone opening into the notches (Figs 3, 4).

Discussion

The shoots of this species closely resemble those of *Sphenolepis kurriana* (Dunker) Schenk in gross morphology and the original attribution by Carpentier is quite understandable. The cuticle however is unique, bearing no resemblance to *S. kurriana* or to any other conifer, fossil or extant, that we have seen. A similar lobed leaf margin has been seen in one other conifer, from the Lower Cretaceous of China, but the cuticles of the two species differ considerably (Zhou Zhiyan, personal communication).

The presence of glands on the abaxial surface, whilst not unknown in conifers, is certainly not common. Many extant members of the Cupressaceae have prominent resin glands but of the species we have studied none bear any resemblance to *Brachyphyllum carpentieri*, where the glands open into the notches of the leaf and involve a complex organization of the epidermal cells.

Wood described by Lemoigne & Demarcq (1967) as *Dadoxylon arduennense* may belong to the same plant as *Brachyphyllum carpentieri*. The silicified wood indicates a tall arborescent plant which was at least 20 cm in diameter at the base of the trunk. The wood is of a type limited to the Jurassic–Cretaceous. It is characterized by septate tracheids which are unknown in modern gymnosperms. The nature of these septa is unclear and indeed it is difficult to conceive what function they may have had in the water transport system. Lemoigne & Demarcq stress that they cannot confirm that the wood is coniferous and comment that the affinity of the wood may be closer to that of the Caytoniales, which are also represented at Féron–Glageon.

If, however, *D. arduennense* should prove to be coniferous it seems probable that the unique structure of the wood combined with the unusual cuticle characters of *B. carpentieri* imply a specific adaptation to particular environmental conditions.

Acknowledgement

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Late Permian plants including Charophytes from the Khuff Formation of Saudi Arabia

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Synopsis

A fossil flora of probable Late Permian age is reported from the Khuff Formation of central Saudi Arabia. The coniferous element is of typical European, Zechstein composition, whilst other elements provide hitherto unrecognized similarities between Permian floras of the western and eastern hemispheres. Stems and reproductive structures of a charophyte – *Palaeonitella tarafiyensis* sp. nov. – represent an unusually complete occurrence of this group in the Permian.

Introduction

The discovery of Permian plants in the clastic facies of the Lower Khuff Formation (El-Khayal, Chaloner & Hill 1980, Lemoigne 1981*a, b*) has stimulated further search of Khuff beds exposures by A. A. El-Khayal. The Lower Khuff has continued to yield a diverse flora which will be further described elsewhere. The present note reports for the first time a markedly different plant assemblage, from the Middle Khuff beds, and one which indicates a later Permian age than the Lower Khuff flora.

The plant remains were collected from a clay quarry 15 km NNE of Buraydah, the capital city of Qasim province, at the base of the escarpment named Jāl al Watāh on the road from Buraydah to Al Tarafīyah (Fig. 1). Exposures in the quarry are approximately at the base of the Khartam escarpment, in the Midhnab Shales which outcrop near the top of the Middle Khuff beds as described by Powers *et al.* (1966: D31). The rock matrix is a deeply weathered grey-brown claystone. Plant megafossils occur sparsely; they are limonitized and lack cuticles, but show some cellular detail of internal structure. Our descriptions are brief, because both the diversity and quality of preservation of the assemblage are limited.

Systematic descriptions

Division TRACHEOPHYTA

The tracheophytes in the present assemblage range from more or less fragmentary foliar remains (Figs 2–4, 11), the majority indeterminable, to relatively well preserved coniferous shoots and cones (Figs 5–8). The indeterminable pinna shown in Fig. 2 is of generalized cycadalean aspect whilst the scale-like foliar organ of Fig. 3 may be pteridospermous. Two specimens of such scales are known, one apparently trilobed and with coarse venation diverging from the assumed base of the scale. At intervals the veins dichotomize and anastomose. At the centre in both specimens there is a more or less well developed scar, suggesting attachment of some other organ, possibly an ovule or reproductive branch. In view of its incomplete preservation we refrain from naming this organ formally, other than as

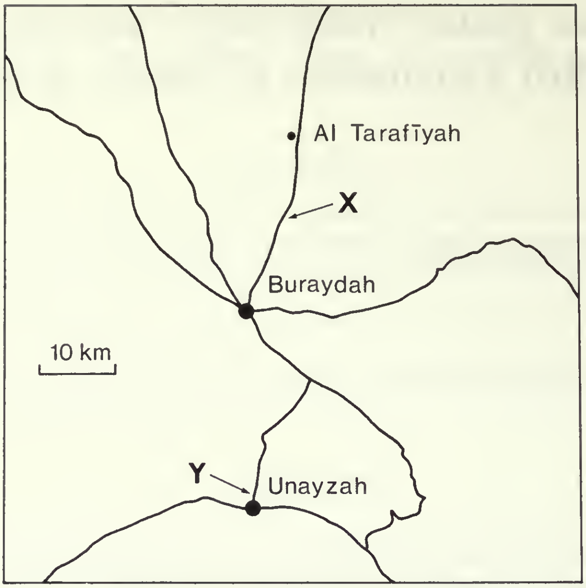

Fig. 1 Road map of Buraydah region showing location of present outcrop at X and of site reported by El-Khayal *et al.* (1980) at Y.

'Problematicum A', in the hope that determined search may yield better specimens. Clearly it is of considerable interest as it displays some hints of glossopterid affinity.

The leaf pinna of Fig. 4, although also of obscure botanical affinity, may be securely named as *Wattia texana* Mamay (1967), originally described from the Early Permian of North America. *Wattia* is possibly of noeggerathialean affinity. Similar fossils occur in the Russian Permian.

These botanically rather obscure remains are associated with well-preserved coniferous leafy shoots that make up about half of the specimens collected. Shoots with relatively long, narrow leaves (Fig. 5) are determined as *Pseudovoltzia* Florin, and those with broad leaves (Fig. 6) as *Culmitzschia* Ullrich, both characteristic of the Late Permian Zechstein floras of Europe (Florin 1963, Schweitzer 1968). A well-preserved female cone (Fig. 7) is also referred to *Pseudovoltzia*. Fig. 8 illustrates the deeply divided cone scale with five fingerlike lobes and a seed (arrowed), as in comparably preserved European material of *Pseudovoltzia liebeana* (Geinitz) Florin (Schweitzer 1963, 1968). We refer the Saudi material to the same species. In view of its limited preservation, however, we cannot entirely rule out similarities with female cones of allied conifers such as *Voltzia* Brongniart and *Glyptolepis* Schimper, which range into the Mesozoic.

Three specimens (Fig. 9) resemble Halle's (1927) 'Problematicum', reported from the Permian of China, though the Saudi material has a more pronounced distal taper to the scars considered to represent points of attachment of sporangia. Halle's material is now known to represent small fragments of detached scales from the possibly noeggerathialean cone *Discinites orientalis* Li *et al.*, *in* 'Gu & Zhi'[1] (1974), which Li & Yao (1980) assign to an Early Permian age. Despite differences from Halle's specimens the Arabian ones fall well within the range of form of *D. orientalis* as figured by 'Gu & Zhi' and are identified with it. *Discinites* is reported also from the Early Permian of North America (Mamay 1954) and species occur widely but sparsely in the Euramerian Carboniferous (Boureau 1964).

Two fragmentary specimens of *Pecopteris* (Fig. 11) were collected, showing evidence of basal fusion of the pinnules and with a simple venation of a kind common in Stephanian and Permian

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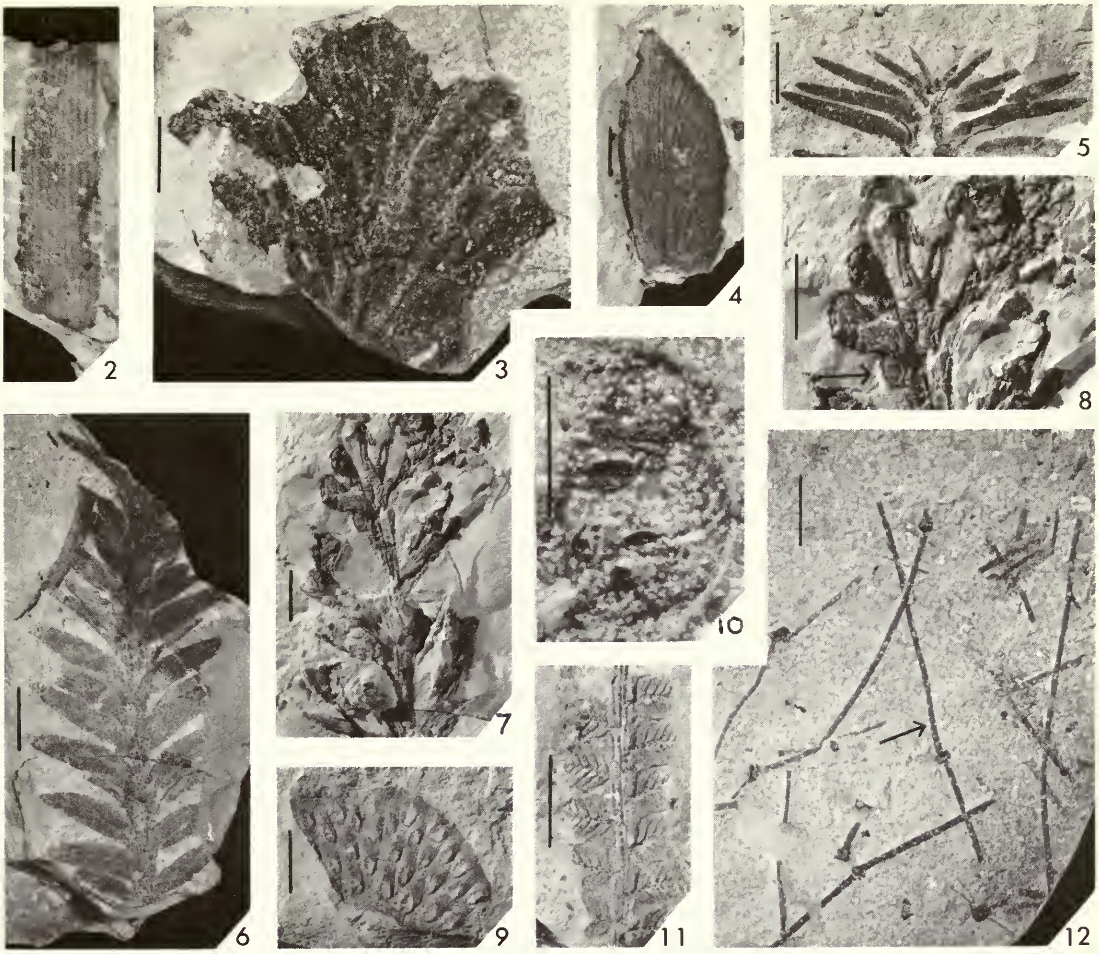
[1] 'Gu & Zhi' represents the contracted and latinized name of an editorial committee called 'Zhongguo *Gu*shengdai *Zhi*wu' (literally, 'Chinese Palaeozoic Plants'), and has been used as an author citation by the Chinese ('Gu & Zhi' 1974: 1). The actual authors, who appear to be the members of the committee ('Gu & Zhi' 1974: 2) are Li Xingxue, Deng Longhua, Zhou Zhiyan, Xu Ren & Zhu Jiagou. If so the full citation given here is redundant and might well be reduced to Li *et al.* alone, bearing in mind however that the authors' names do not appear on the title page of the work.



Figs 2–12 Plant fossils from the Middle Khuff beds, 15 km NNE of Buraydah, Permian of central Saudi Arabia. Scale bars each represent 5·0 mm except for Fig. 10 where the bar represents 0·5 mm. Fig. 2, indeterminable pinna. Fig. 3, Problematicum A. Fig. 4, *Wattia texana* Mamay. Fig. 5, *Pseudovoltzia liebeana* (Gienitz) Florin, foliage. Fig. 6, *Culmitzschia* sp. Figs 7, 8, *Pseudovoltzia liebeana* (Geinitz) Florin: Fig. 7, female cone; Fig. 8, female cone scale at higher magnification, with ovule arrowed. Fig. 9, *Discinites orientalis* Li *et al. in* 'Gu & Zhi'. Figs 10, 12, *Palaeonitella tarafiyensis* sp. nov.: Fig. 10, oosporangium (scale bar 0·5 mm), see also Fig. 13; Fig. 12, stems with **holotype** stem arrowed, BM(NH) Palaeontology Dept. no. V.60935. Fig. 11, *Pecopteris* sp. indet. All specimens except those of Figs 10, 12, are in the Geology Department, King Saud University, Riyadh.

pecopterids. In the absence of pinna terminals and of larger fragments indicating the range of variation within the frond, we do not attempt specific identification.

All the tracheophyte specimens are housed in the Geology Department, King Saud University, Riyadh.

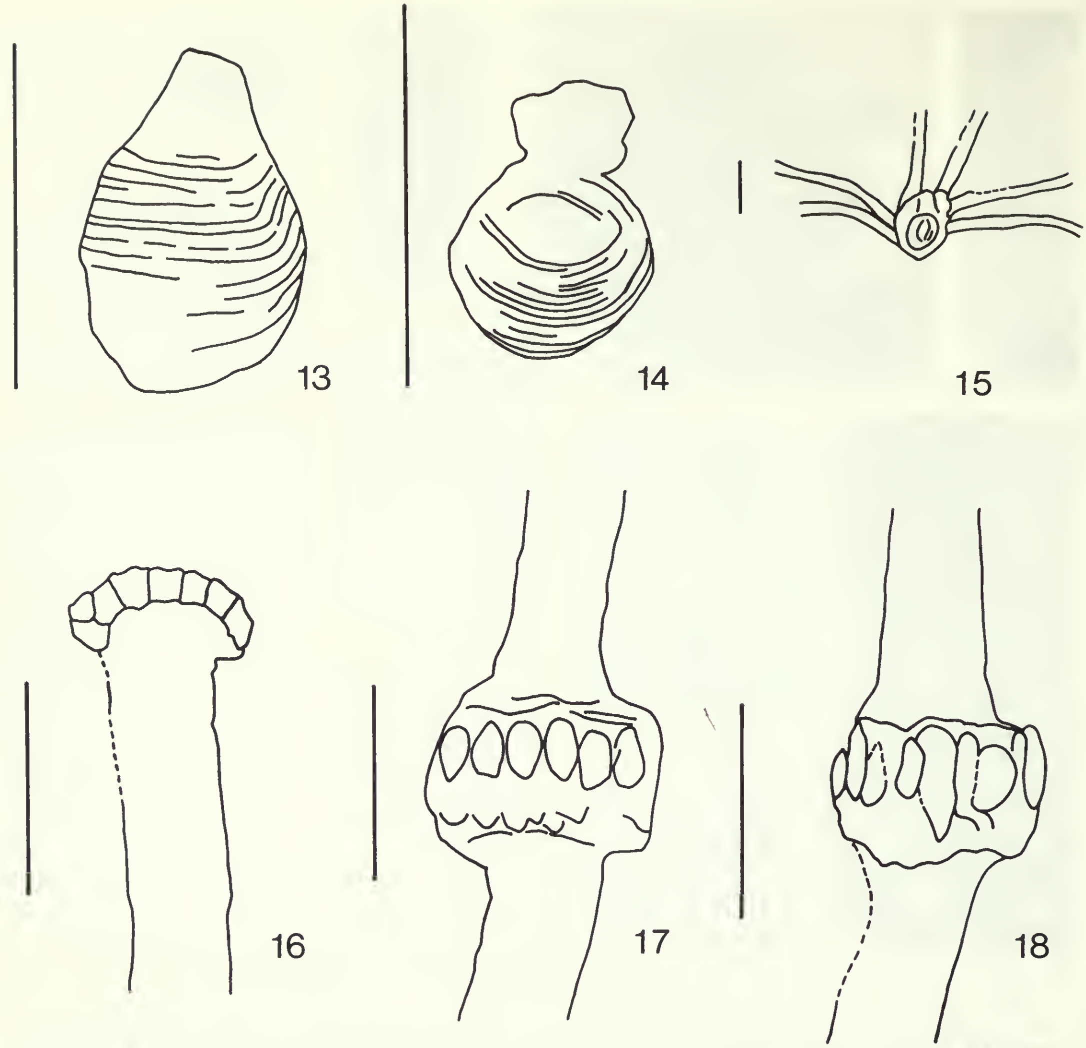
Plesion **CHAROPHYTA**

Genus ***PALAEONITELLA*** Pia *in* Hirmer, 1927

Palaeonitella tarafiyensis sp. nov.

Figs 10, 12–18

Description. Stems (broken during fossilization) exceeding 27 mm in length, internodes smooth and without preserved cortical cells, up to 0·7 mm wide; nodes occurring at intervals of



Figs 13–18 *Palaeonitella tarafiyensis* sp. nov., drawings on photographs. All from BM(NH) Palaeontology Dept. no. V.60935, scale bars each representing 1·0 mm. Figs 13, 14, oosporangia, Fig. 13 shown also in Fig. 10. Fig. 15, node compressed in plane of the whorl, showing six branches. Figs 16–18, portions of stem compressed laterally, showing nodes with basal scars of branches.

1–25 mm or more, swollen to about twice the width of the internodes. Nodes bearing a single ring of branches. (Branches seen when compressed in the plane of the whorl as in Fig. 15, whilst in denuded stems compressed sideways their points of attachment are represented by a ring of elliptical basal scars as in Figs 16–18). Obscure indications of additional cells or possibly stipulodes occur above or below the branch scars (Fig. 17). Branches 12–16 per node (count based mainly on numbers of basal scars). Reproductive structures (oosporangia) in intimate association but not seen definitely attached to stems, urn shaped, 1·0 mm long × 0·5 mm wide at broadest point, striated helically in sinistral direction, about 15–20 such stria per oosporangium; actual number of coiled cells unknown (Figs 10, 13, 14). (Superficially the coiling of striae looks dextral, since the surface visible is a mould of the oosporangium).

Holotype. V.60935; specimen arrowed in Fig. 12 and portion shown also in Fig. 17.

Material. Several fragments, as shown in Fig. 12, all on one block only and apparently limited to one bedding plane.

Locality and horizon. As indicated in the Introduction, p. 105.

Diagnosis. Differs from the only other species of the genus, *P. cranii* (Kidston & Lang) Pia *in* Hirmer, in its wider stems and in having branches that apparently lack septae.

Preservation. The botanical as opposed to stratigraphic and palaeobiogeographic interest of the Middle Khuff flora is considerably enhanced by these charophytes. The material represents an early and exceptionally complete occurrence of plants of this group, which elsewhere is known as fossils almost solely from reproductive structures. There are notably few records from the Permian (Peck & Eyer 1963).

In the Saudi material vegetative remains occur closely association with reproductive organs. Their mode of preservation as impression fossils yields considerably less detailed information than is available from the usual preservation of charophytes as petrifactions. However, the preservation is sufficiently detailed to indicate that the Saudi stems were ecorticate, resembling those described by Kidston & Lang (1921) from the Devonian and by Ishchenko & Saidakovsky (1975) from the Silurian.

Nomenclature. Since assignment of the Saudi specimens to a family is problematic we use a form genus. The name *Palaeonitella* was applied by Kidston & Lang (1921) to vegetative remains from the Rhynie Chert, some at least of which clearly resemble those of charophytes but with no oosporangia. The internodes are ecorticate. Unfortunately Kidston & Lang applied the name so informally that it cannot be attributed to them – they named their material *Algites (Palaeonitella) cranii* – and the name was only validated by Pia *in* Hirmer (1927). Horn af Rantzien (1956) discusses the nomenclatural details, with which we agree fully, though we believe the citation for the generic name should be in the form given here rather than as *Palaeonitella* (Kidston & Lang) Pia. This citation more properly belongs to the species name *Palaeonitella cranii*.

Although the attribution of Kidston & Lang's material to the Charophyta is open to some doubt in the absence of reproductive organs (Groves 1933), the name *Palaeonitella* is used here in order to limit gratuitous inflation of names (see Harris, 1962–3). We use it for any uncorticated stems resembling those of Charophyta and of which the oosporangia may be known – as in *P. tarafiyensis* – or may not be known – as in *P. cranii* – but of which the oosporangia even when known do not permit narrower determination than to the Charophyta as a whole. (*Charaxis* Harris is available for corticate stems). We note in passing that only the largest specimens of *P. cranii* fall within the range of stem width represented by the slenderest species of extant *Nitella*, whereas *P. tarafiyensis* is typical of the majority of extant species.

Such limited detail of the oosporangia as is preserved in *P. tarafiyensis* neither refutes nor supports assignment to the Porocharaceae, which would be the predicted familial determination based on the age of the material (Grambast 1974). Further specimens are needed.

Palaeoecology. These Permian stems are remarkably like stems of living species in size and known morphology, resembling ecorticate species of extant *Chara, Nitella* and *Tolypella*. Charophyta are of considerable palaeoecological interest since all living species are limited to fresh or brackish water environments, though some earlier Palaeozoic representatives are believed to have been shallow-marine (Racki 1982). Notably in this present fossil flora the charophyte remains are associated with fresh-water bivalves, suggesting a fresh-water – perhaps lacustrine – environment of deposition; presumably they were not transported far from their place of growth whereas other species in the flora are clearly drifted. There is no evidence to suggest *P. tarafiyensis* was lime-encrusted in life, in contrast to most described fossil charophytes and to many living species. The Middle Khuff matrix is in fact gypsiferous and lacks calcium carbonate.

Discussion

Floristic affinities. The affinities of the assemblage as a whole are no less intriguing than those of the Lower Khuff flora (El-Khayal *et al.* 1980). In that flora, *Pecopteris, Fascipteris, Lobatannularia, Cordaites* and *Marattiopsis* are conspicuous elements whilst conifers are lacking. The Middle Khuff flora is in stark contrast: out of the genera just mentioned only *Pecopteris* occurs, and that inconspicuously, whereas the strong coniferous element (*Pseudovoltzia, Culmitzschia*) is in marked contrast to the earlier assemblage. Such sharp differences in plant assemblages having rather slight age differences are unusual and surely signify a strong degree of environmental control, either ecologically or sedimentologically or both.

Almost all the Middle Khuff species are unknown in floras of roughly comparable age from the Middle East but closely resemble those found in floras from far distant localities, mainly in the northern hemisphere Permian. The only hint of Gondwana affinities is provided by the scale-like foliar organ Problematicum A (p. 106), though that in itself – if its glossopterid affinities were substantiated – would be of great interest. *Wattia* is described from the Early Permian of Texas, U.S.A., *Discinites* ranges into the Early Permian of China, Korea and North America, but *Pseudovoltzia* and *Culmitzschia* are characteristic of the European Late Permian (Florin 1963). Clearly this flora fills a gap between the Permian floras of the Euramerian and Cathaysian areas of Chaloner & Meyen (1973) and thus represents a mixed flora. Lemoigne (1981*a*, *b*) argues similarly for the Lower Khuff flora reported briefly by El-Khayal *et al.* (1980). Lemoigne's perceptions of a strong Cathaysian element in that flora, extending vigorously along the shores of Tethys, rest however largely on the validity of his determinations and interpretations. We hope the further studies now in progress by Wagner & El-Khayal may resolve taxonomic problems raised by El-Khayal *et al.* (1980) and by Lemoigne's 1981*b*.

STRATIGRAPHY. That the Middle Khuff assemblage reported here is younger than the Lower Khuff flora is certain from the field relations. If the strong coniferous element is emphasized at the expense of other taxa, the plant megafossils suggest a probable Late Permian age. Nevertheless, in such strictly palaeobotanic terms, exact age assignment may be regarded as problematic for a number of reasons. Firstly, the floras of the Arabian peninsula, as at Hazro in Turkey, are regionally unique. They fill gaps and thus obscure formerly clearly perceived boundaries between floral provinces, yet have a character of their own. Secondly, Permian floras worldwide are rather poorly known. Whilst they therefore represent a challenging and stimulating research topic, in which a great deal is still to be learnt, stratigraphic ranges of Permian megafossil plants are as yet poorly documented. The literature, too, is scattered. Thus, if the present floras in Saudi Arabia are in fact both Late Permian, they considerably extend the ranges of *Wattia* and *Discinites* whilst the ranges of *Marattiopsis, Pseudovoltzia* and other species remain as previously understood by Florin (1963), Burago (1977) and others. For these reasons the initial report by El-Khayal *et al.* (1980) on the Lower Khuff flora cautiously suggested a rather broad age range: from not older than Westphalian (Upper Carboniferous) to not younger than Early Permian, rather than a more precise age assignment. Others, notably Lemoigne (1981*a*, *b*) have felt able to provide a more detailed age range based on the palaeobotanical evidence, attributing a degree of precision to palaeobotanical dating which in our view may be premature for such limited floras in a Permian context. It also takes little account of a third limitation, the likely environmental as opposed to stratigraphic control over such marked changes as occur between the Lower and Middle Khuff floras. Nonetheless, by the same argument, we do not consider Lemoigne's specifically Late Permian age assignment for the Lower Khuff flora unreasonable. If pressed to give a narrower age range for the flora, however, we now tentatively favour an early Late Permian age for the Lower Khuff flora, based entirely on the plant data.

The evidently somewhat vexed question of the age of the Lower Khuff flora has been further discussed recently by Sharief (1982*a*, *b*) and Ibrahim (1982). In view of the limitations of palaeobotanic data when considered in isolation, referred to above, we believe Ibrahim overemphasizes the botanically-based age assignment of El-Khayal *et al.* (1980). Moreover, Popper (1959), Lakatos (1970) and others have stressed the importance of using independent lines of evidence to test and thus critically to evaluate scientific hypotheses. As Sharief (1982*b*) rightly points out, independent evidence is available from palynology – though regrettably unpublished ('Aramco' 1975). A Late Permian age is also indicated by the calcareous algae

(Rezak 1959). Such evidence, whilst not in itself necessarily superior to megafossil palaeobotanic evidence, uniformly suggests a Late Permian age for the Khuff Formation. Present evidence, therefore, all seems to favour a Late Permian age for both the Lower and Middle Khuff floras.

To clarify the stratigraphic nomenclature used in this discussion we should emphasize that usage of the term 'Khuff Formation' follows that of Powers *et al.* (1966), in including the Unayzah plant bed within the Lower Khuff. El-Khayal & Wagner (in preparation) argue that the Unayzah beds should be separated off from the Khuff as a separate Formation.

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British Carboniferous Edrioasteroidea (Echinodermata)

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Synopsis

The entire British fauna of Carboniferous edrioasteroids is revised and redescribed and a newly discovered hardground, where edrioasteroids are exceedingly abundant, is described. All belong to the family Agelacrinitidae and three genera and four species are recognized. Two of the genera, *Lepidodiscus* and *Postibulla*, are known from North America but the third, *Stalticodiscus* (type species *Lepidodiscus milleri*), is new. The new species *Postibulla neglecta* is described. Growth and plate ultrastructure of *Stalticodiscus milleri* have been studied using scanning electron microscopy. This species was able to orientate itself in currents and possibly lived in bimodal (i.e. tidal) current regimes with the anterior–posterior axis at right angles to the flow of water.

Introduction

It is now more than a hundred years since the first edrioasteroid was described from the Carboniferous of the British Isles, yet they have remained extremely rare fossils known from only a few localities in northern England. Three species have been described with varying accuracy, *Lepidodiscus lebouri* Sladen 1879, *Lepidodiscus milleri* Sharman & Newton 1892 and *Lepidodiscus fistulosus* Anderson 1939. This last species was thought so distinct that Regnéll (1950) erected the genus *Anglidiscus* for it.

The only edrioasteroids known from the Carboniferous are isorophids belonging to the family Agelacrinitidae. These, like all isorophids, were sessile and lived attached to hard substrates. Only the upper (ventral) surface is calcified and the skeleton consists of imbricate or tesselate plates set within a soft tissue membrane. Upon death, the theca rapidly dissociates as the soft tissue decays and so, to be preserved, edrioasteroids must be buried alive or within a very short time of death. However, isorophids lived on hard substrates in areas of active erosion where they stood very little chance of being preserved. It is therefore only under exceptional circumstances that we ever find them in the fossil record. Until now, most specimens found in the British Carboniferous have been single individuals attached to shells, presumably living at the limits of tolerance offshore to the main population. The discovery of a new horizon in the Lower Carboniferous of Cumbria yielding an abundance of well-preserved edrioasteroids is an unusual and important find and I am extremely grateful to Dr Paul Taylor of the British Museum (Natural History) who brought this occurrence to my notice.

The discovery prompted a re-examination of the previously-described species, and it soon became apparent that published descriptions were unsatisfactory. The contemporary American fauna is now well known from the work of Bassler (1936), Kesling (1960) and especially Bell (1976*a*). This paper sets out to revise the British Carboniferous edrioasteroids.

Occurrence

All the British Carboniferous edrioasteroids come from the Early Asbian stage of the Dinantian. American Carboniferous edrioasteroids have been discovered at various levels throughout the Mississippian and it is not at all clear why the British fauna should be so restricted in its occurrence. There are five localities that have yielded edrioasteroids, all of them in

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northern England. I am indebted to Dr W. H. C. Ramsbottom of the Institute of Geological Sciences, Leeds, who supplied me with accurate stratigraphic data on these localities, as follows.

(i) The River Irthing, one mile (1·6 km) east of Waterhead, Northumberland (National Grid reference (approx.) NY 635685). This occurrence was reported by Sharman & Newton (1892) and Ramsbottom (1970: 172). Here the Millerhill Limestone outcrops as a strike section for some distance. This limestone is divided into an upper and a lower unit but it is not known from which of these the single edrioasteroid came. The Millerhill Limestone lies within the Upper Border Group and is middle Early Asbian in age. One specimen of *Stalticodiscus milleri* (Sharman & Newton) has been collected from here.

(ii) The River Irthing, ⅝ of a mile (1 km) south of Lampert, Northumberland at the foot of Linen Sike (NY 683735). A specimen of *Stalticodiscus milleri* (Sharman & Newton) has been found here in a shelly calcareous shale that lies just above the Millerhill Limestone. This is again middle Early Asbian in age. It was recorded by Sharman & Newton (1892) and Ramsbottom (1970: 172).

(iii) A horizon 103 ft 6 in (31·5 m) down the Hetton House borehole (NU 042296) yielded some 33 edrioasteroids (Anderson 1939). These come from a siltstone with calcareous bands situated about half way up the Scremerston Coal Group and Early Asbian in age, probably not very far from the Millerhouse Limestone horizon. The fauna consists mainly of *Lepidodiscus* cf. *squamosus* Meek & Worthen with subsidiary *Postibulla neglecta*.

(iv) An impure limestone outcropping in the River Rede, where it forms a low waterfall just north of the bridge above the village of East Woodburn, Northumberland (NY 901877). Here was found the only known specimen of *Lepidodiscus lebouri* Sladen (Sladen 1879; Miller 1887: 41). This horizon is approximately 900 ft (275 m) below the Redesdale Limestone (not 700 ft as stated by Miller) and lies close to the top of the Early Asbian.

(v) The road cutting at Penruddock on the north side of the A66 road just at the end of a stretch of dual carriageway some 6 miles (9·5 km) west of Penrith, Cumbria (NY 438275). The succession here is given in Fig. 1. Edrioasteroids occur crowded on the upper surfaces of bored and encrusted micritic concretions which can be several feet in diameter. This horizon had obviously been exposed for a considerable time before being smothered by a rapid influx of mud. In general the encrusting bryozoa and inarticulate brachiopods are found on the undersides of the concretions whereas acrothoracic barnacle borings and edrioasteroids are found on the upper surfaces. Concretions with abundant borings tend not to have edrioasteroids and *vice versa*.

The brachiopods from this locality suggest an Asbian age, according to Dr C. H. C. Brunton of the BM(NH) (personal communication). The foraminifera, which include *Koninckopora inflata* (de Koninck), *Eostaffella parastruvei* Rauser, *Archaeodiscus* sp. and *Globoendothyra*, were identified by Dr A. R. E. Strank of the I.G.S., Leeds, and indicate a Holkerian or Early Asbian age. Dr W. H. C. Ramsbottom informs me that the beds at this locality probably belong to the undivided Sixth/Seventh Limestones, in the lower part of the Early Asbian.

Taxonomy

Order **ISOROPHIDA** Bell, 1976

Suborder **ISOROPHINA** Bell, 1976

Family **AGELACRINITIDAE** Chapman, 1860

Genus ***LEPIDODISCUS*** Meek & Worthen, 1868

[= *Anglidiscus* Regnéll, 1950]

Lepidodiscus cf. ***squamosus*** Meek & Worthen, 1868

Figs 2–5, 8

1868 *Agelacrinites (Lepidodiscus) squamosus* Meek & Worthen: 357–358.
1939 *Lepidodiscus fistulosus* Anderson: 68 (part).

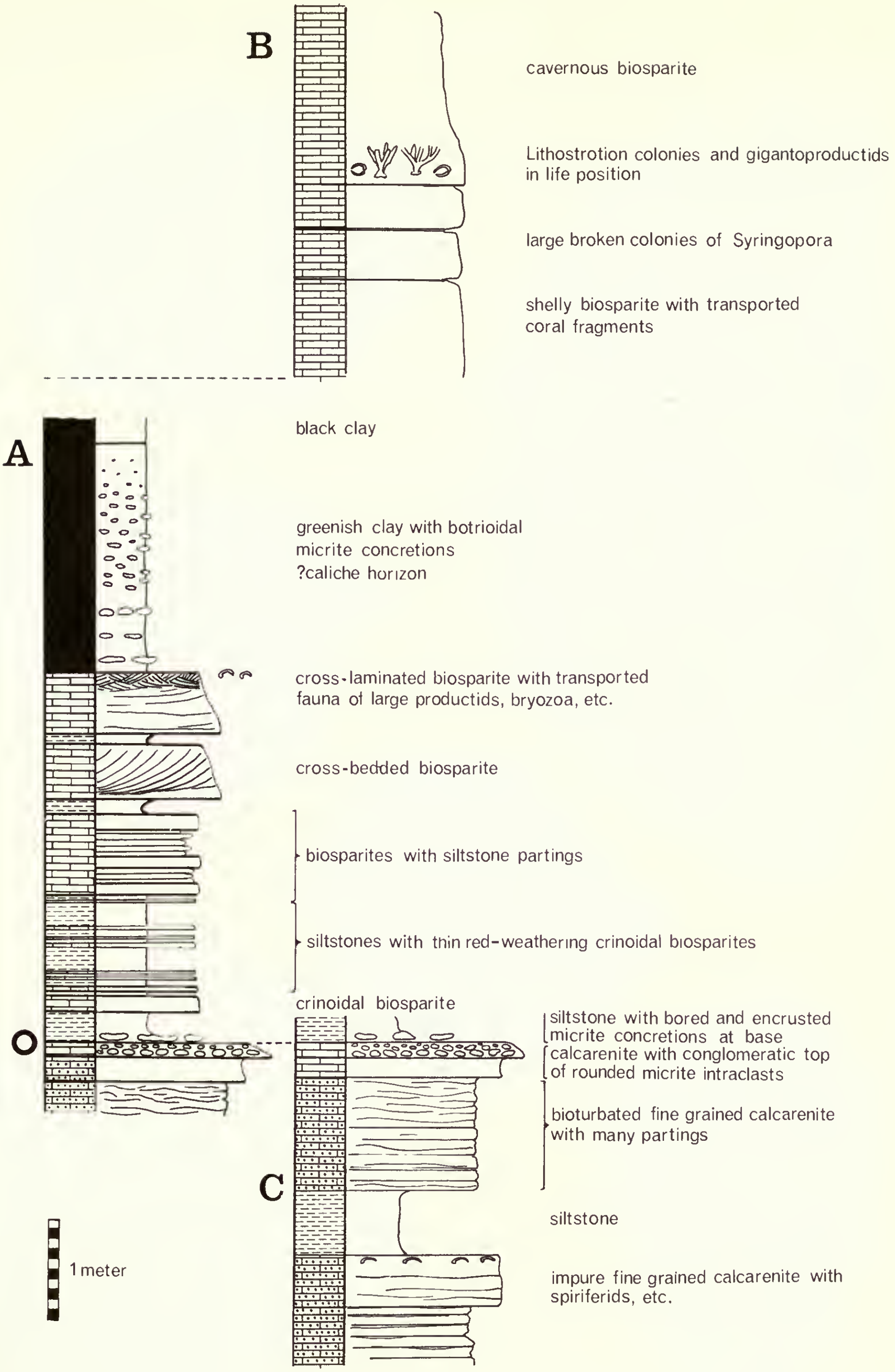
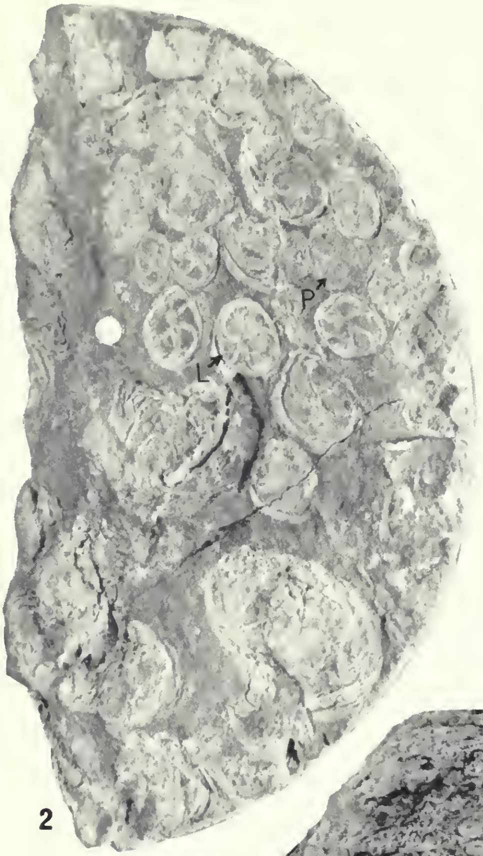

B
cavernous biosparite
Lithostrotion colonies and gigantoproductids in life position
large broken colonies of Syringopora
shelly biosparite with transported coral fragments
A
black clay
greenish clay with botrioidal micrite concretions ?caliche horizon
cross-laminated biosparite with transported fauna of large productids, bryozoa, etc.
cross-bedded biosparite
biosparites with siltstone partings
siltstones with thin red-weathering crinoidal biosparites
crinoidal biosparite
o
siltstone with bored and encrusted micrite concretions at base
calcarenite with conglomeratic top of rounded micrite intraclasts
bioturbated fine grained calcarenite with many partings
C
siltstone
impure fine grained calcarenite with spiriferids, etc.
1 meter

Fig. 1 Sedimentary log for succession exposed at Penruddock road cutting, near Penrith (loc. v). A, succession towards the west end of the road cutting. B, succession in the old quarry immediately above the road cutting. C, succession towards the east end of the road cutting, east of the an obvious fault. o – the horizon with edrioasteroids encrusting limestone concretions.



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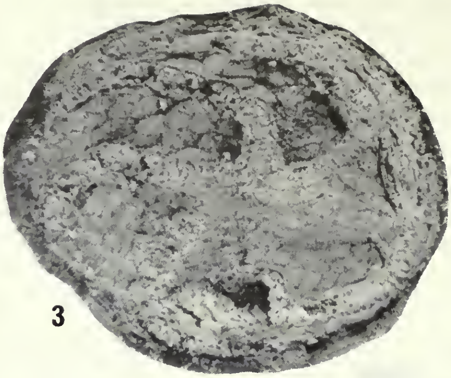

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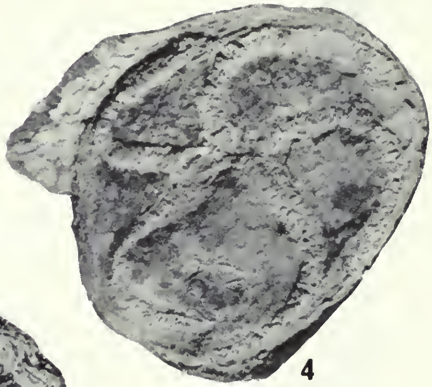

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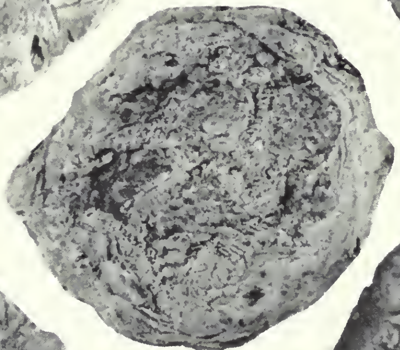

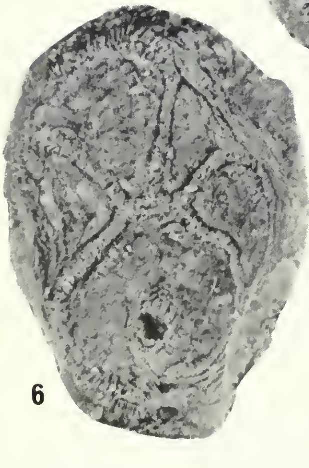

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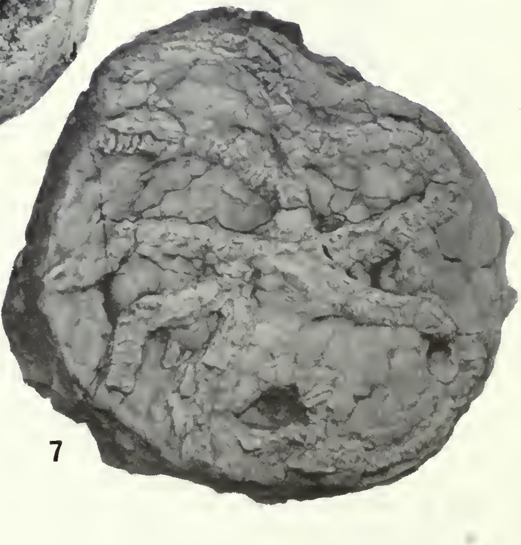


7

1950 *Anglidiscus fistulosus* (Anderson); Regnéll: 6 (part).
1966 *Anglidiscus fistulosus* (Anderson); Regnéll: U162 (part).
1976*a* *Lepidodiscus squamosus* Meek & Worthen; Bell: 253–257 (q.v. for full bibliography of American records).

DIAGNOSIS. An agelacrinitid with a clavate theca and long curved ambulacra. Ambulacra I–IV curve sinistrally, V curves dextrally (rarely all curve sinistrally). Cover plates arranged cyclically in groups of six or seven. Oral area composed of many cover plates continuous with ambulacral series. Hydropore rise in posterior right of oral area (type VI of Kesling, 1960), posterior side formed of many plates. Interambulacral plates squamose, imbricate. Periproct an anal valve of two cycles of plates. Flooring plates uniserial, imbricate.

MATERIAL. Institute of Geological Sciences no. 60235. Half of a six-inch (150mm) core with parts of 31 specimens.

LOCATION AND AGE. Hetton House bore-hole, Northumberland (loc. iii, p. 114). Early Asbian, Dinantian.

DESCRIPTION. The British specimens of this species all come from one piece of bore-hole core. There are parts of 31 specimens of which only 15 are tolerably complete. A further two specimens belong to the genus *Postibulla* and are described later. All the specimens are preserved upside down, revealing the inner surface of the theca. Latex moulds were made of three of the better-preserved specimens.

In life the specimens must have been tall and domal in shape but most are preserved in the contracted state. In all but one specimen ambulacra I–IV curve sinistrally and ambulacrum V curves dextrally. There is, however, one (? abnormal) specimen in which all five ambulacra curve sinistrally (Fig. 8). Distally the ambulacra curve round to become parallel to the periphery. The arrangement of cover plates is nowhere clear but cycles of three or four large plates together with small intercalated plates can be seen. This seems comparable with the cyclical cover plate arrangement seen in the better-preserved American material. Ambulacral flooring plates are uniserial and imbricate. Contrary to Anderson's (1939) findings, the flooring plates are totally imperforate. Preservation around the oral area is too poor to permit a detailed analysis of the cover plate arrangement but it is clear that the oral cover plates are continuous with the ambulacral cover plates and that no enlarged oral primary cover plates are present. Oral cover plates are numerous and small. There is a prominent hydropore bulge situated to the posterior of the oral area adjacent to ambulacrum V. The posterior side of this bulge is formed by a number of small plates.

Interambulacral areas are composed of numerous squamose, imbricate plates that become noticeably smaller towards the ambulacra and around the anal cone. The inner surface of these plates is composed of a coarse-meshed stereom which led Anderson (1939) to believe mistakenly that they were perforate. The anal cone lies roughly central in interambulacrum 5 and consists of a double circlet of rather elongate triangular plates. The peripheral rim is of standard appearance.

Figs 2–6 IGS no. 60235, the half core from which Anderson described *Lepidodiscus fistulosus*. Fig. 2, the whole specimen, ×0·8; L = lectotype of *Anglidiscus fistulosus* (= *Lepidodiscus* cf. *squamosus*) (see Fig. 4), P = holotype of *Postibulla neglecta* sp. nov. (see Fig. 6). Fig. 3, *Lepidodiscus* cf. *squamosus* Meek & Worthen, latex cast of specimen xxix of Anderson (1939: 70) situated to the lower right of the letter P in Fig. 2, ×4. Fig. 4, *Lepidodiscus* cf. *squamosus* Meek & Worthen, natural mould, **lectotype** of *Anglidiscus fistulosus* (Anderson) (L in Fig. 2), ×4. Fig. 5, *Lepidodiscus* cf. *squamosus* Meek & Worthen, latex cast of specimen xxii of Anderson (1939: 70), an abnormal individual with all five arms curving sinistrally, ×4; see Fig. 8. Fig. 6, *Postibulla neglecta* sp. nov., **holotype** (P in Fig. 2), number xxvi of Anderson (1939: 70), ×4; see Fig. 11.

Fig. 7 *Lepidodiscus lebouri* Sladen, BM(NH) E29330, holotype ×2½. See Fig. 9.

Figs 2–7 whitened with ammonium chloride sublimate.

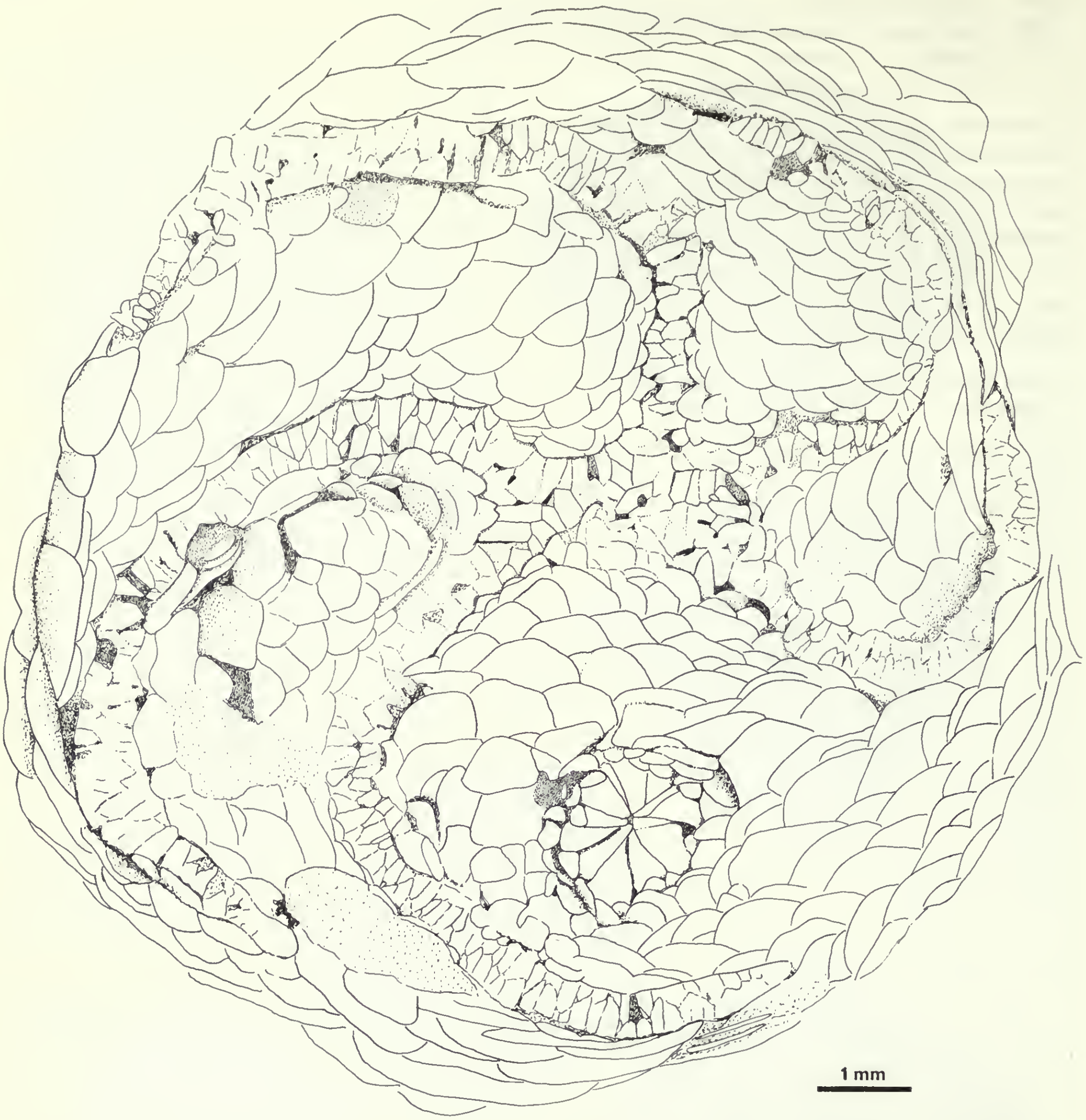


Fig. 8 *Lepidodiscus* cf. *squamosus* Meek & Worthen. Camera-lucida drawing of Anderson's specimen xxii (IGS no. 60235), an abnormal individual with all five arms curving sinistrally. See Fig. 5.

Discussion. One rather unusual feature of this material is that the specimens are preserved in a siltstone with thin calcareous bands. They are not all preserved on one level but are present at two levels a few millimetres apart. It is obvious that the sediment was not lithified into a hard ground at this horizon and that the edrioasteroids were not attached to the sediment, since they have all separated to reveal their inner surfaces. The most likely explanation for this is that the edrioasteroids were originally attached to one or more fronds of free-standing alga which became detached and transported before being rapidly buried. Decay of the alga left the edrioasteroids buried without trace of the substratum to which they were attached.

The fact that the specimens only show the inner surface of their thecal plating, together with the rather poor state of preservation, makes the interpretation of their structure difficult. This probably explains why Anderson's (1939) original description contains a number of basic misconceptions. No holotype of *Lepidodiscus fistulosus* was designated by Anderson and only a general reconstruction was given. However, as Anderson's reconstruction was supposedly based mainly on his specimen (1939: 70) viii, this is here designated the **lectotype**. Anderson believed that all the edrioasteroids on this block belonged to *L. fistulosus*, but although most individuals, including the lectotype, are here referred to *Lepidodiscus* cf. *squamosus*, two belong to the genus *Postibulla*. There is no evidence that the flooring plates are pierced by pores, nor can I find the purported median groove on the flooring plates. More importantly, the oral plating arrangement shown in Anderson's reconstructoin is incorrect. Anderson (1939: 78–79) assumed that 'the mouth . . . is covered by three peristomal plates as in *A(gelacrinites) pileus* Hall, though only the posterior one can be recognized'. I can only think that he mistook the large hydropore plate seen in one of the specimens of *Postibulla* for the posterior primary oral cover plate (Fig. 11, p. 122). The reconstructed arrangement of ambulacral cover plates is also incorrect.

Lepidodiscus fistulosus was referred to the family Hemicystitidae by Regnéll (1950), who created the new genus *Anglidiscus* for it. He did this on the strength of Anderson's description and without having seen the original specimens. As the species is synonymous with *Lepidodiscus squamosus, Anglidiscus* is a junior synonym for *Lepidodiscus*.

In America, *Lepidodiscus squamosus* is known from Indiana and Pennsylvania in beds of the Kinderhookian and Osagean Series (Bell 1976*a*) which pre-date the British find (George *et al.* 1976). There *Lepidodiscus* is a fairly long-ranged genus occurring throughout the Mississippian. *L. squamosus* differs from all other species referred to this genus in having imbricate rather than abutting flooring plates. Compared with American material, in the British specimens of *L.* cf. *squamosus* the imbrication of the flooring plates is slightly less pronounced and there is somewhat less of an overlap of the two posterior ambulacra behind the periproct. Otherwise the two are comparable as far as can be made out.

The one specimen in which all five ambulacra curve in the same direction (Fig. 8) is in all other respects identical to the remaining specimens of *L.* cf. *squamosus*. It is clearly just an abnormal individual within the population.

Lepidodiscus lebouri Sladen, 1879

Figs 7, 9, 10

1876 *Agelacrinites (Lepidodiscus) squamosus* Meek & Worthen; Lebour: 22.
1879 *Lepidodiscus lebouri* Sladen: 745; pl. 37, figs 1–4.
1936 *Lepidodiscus lebouri* (Sladen); Bassler: 20; pl. 1, fig. 19.

MATERIAL. Holotype and only known specimen British Museum (Natural History) Palaeontology Dept. no. E29330.

LOCATION AND AGE. From the River Rede near East Woodburn, Northumberland (loc. iv, p. 114). Early Asbian, towards the top of the sub-stage.

DIAGNOSIS. Large clavate species of *Lepidodiscus* with long, curved ambulacra: ambulacra I–IV curve sinistrally, ambulacrum V curves dextrally. Cover plates arranged in cycles of six. Anal cone lies in interambulacrum 5 close to ambulacrum I and is bordered distally by the tip of ambulacrum V. Hydropore included to the posterior right of the oral area, bounded posteriorly by a few small plates. Interambulacra composed of numerous tesselate plates.

DESCRIPTION. There is only one specimen known of this species and it is preserved ventral surface uppermost. Peripherally the plating curves underneath suggesting that in life the theca was clavate in shape. It is a large edrioasteroid with a diameter of 25 mm. There are six

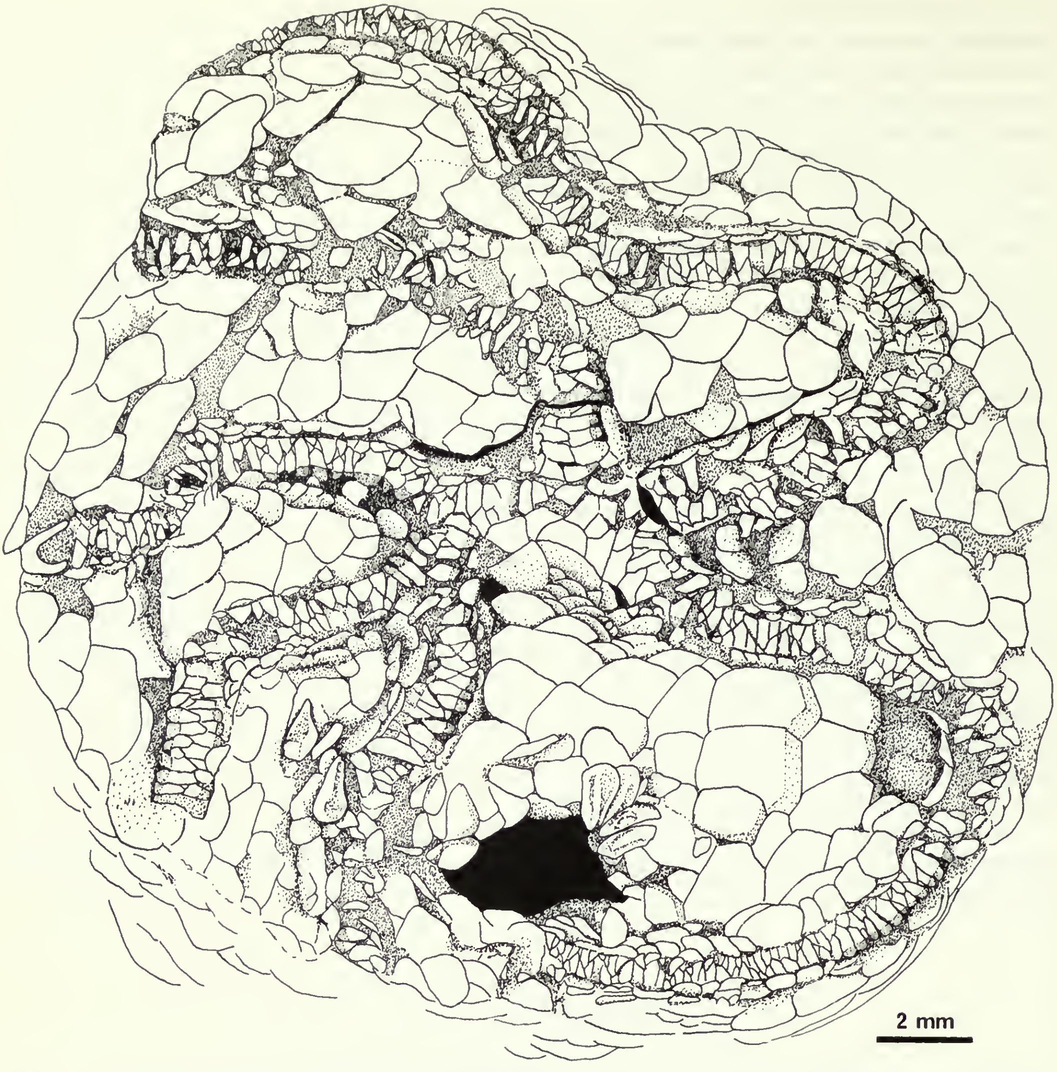


Fig. 9 *Lepidodiscus lebouri* Sladen. Camera-lucida drawing of the holotype BM(NH) no. E29330. See Fig. 7.

ambulacra, an abnormality produced by ambulacrum I bifurcating shortly after it had separated from ambulacrum II. Ambulacrum V curves dextrally; all other ambulacra curve sinistrally. The oral area is covered by a large number of cover plates that are continuous with the ambulacral cover plates. Unfortunately the plating is somewhat disrupted (Fig. 9) and the exact arrangement cannot be determined. There are no distinctly larger primary cover plates. Ambulacral cover plates are arranged in cycles of six, three or four larger plates plus two or three tiny occluded cover plates in each cycle (Fig. 10). The perradial suture is markedly zigzag except over the oral area and the ambulacra form obvious ridges on the theca. Cover plates are small, triangular and wedge-shaped in cross section. The larger cover plates in each cycle have intrathecal extensions. Towards the distal end of the ambulacra the small occluded cover plates are lost from the cycles. Ambulacral flooring plates are largely covered, but can be seen in cross section in ambulacrum II. They are uniserial and U-shaped in cross section.

The hydropore belongs to type VI of Kesling (1960). It lies in the right posterior side of the oral area and is bounded by cover plates anteriorly, and posteriorly by a small number of (?)

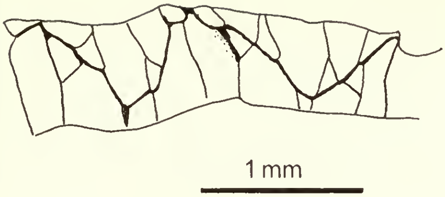


Fig. 10 Camera-lucida drawing of cover plate arrangement from ambulacrum II of the holotype of *Lepidodiscus lebouri* (BM(NH) no. E29330).

interambulacral plates. The posterior slope to the oral area is steep and formed by two rather large plates together with a number of smaller plates (Fig. 9).

Interambulacral areas are broad and composed of numerous sub-polygonal tesselate plates. These are relatively thick and imbricate adorally. The interambulacral plates are largest near the centre of each area but become obviously smaller close to ambulacra and around the periproct.

The periproct is largely disrupted and individual plates of the anal cone lie scattered nearby. It is situated in the more distal left-hand side of interambulacrum 5, fairly close to ambulacrum I. The tip of ambulacrum V curves round to lie just posterior to the periproct.

Discussion. There are three species of *Lepidodiscus* known from North America (Bell 1976*a*): *L. squamosus* Meek & Worthen, *L. laudoni* (Bassler) and *L. sampsoni* (Miller). *L. lebouri* differs from *L. squamosus* in having tesselate ventral plating and a clavate body. It differs from *L. sampsoni* in having curved ambulacra: the ambulacra in *L. sampsoni* form long, straight ridges on the ventral surface. *L. lebouri* comes closest to the common North American species *L. laudoni*, which is found throughout the Mississippian ranging from the Kinderhookian to the Chesterian. Unfortunately the plating of the pedunculate zone and the internal aspect of the ambulacral flooring plates are unknown for *L. lebouri*. In other features the two species are closely comparable, save for the abnormal sixth ambulacrum in *L. lebouri* and the presence of two prominent plates forming the posterior slope to the oral area. Although *L. lebouri* will probably prove to be conspecific with *L. laudoni*, the two species are here retained as distinct until further British material becomes available for comparison. In uniting the two species *L. laudoni* would become a junior synonym, which would have the undesired consequence of making the holotype of this common species a six-armed abnormality.

Sladen's (1879) original description was comprehensive and for the most part accurate, as was the accompanying illustration. His interpretation of the arrangement of ambulacral cover plates is not quite correct, however, as he failed to notice the presence of small occluded plates. Sladen quite correctly recognized the species' distinctness from *Lepidodiscus squamosus* and '*Lepidodiscus*' *(Discocystis) kaskaskiensis*.

Genus ***POSTIBULLA*** Bell, 1976*a*

Postibulla neglecta sp. nov.
Figs 2, 6, 11

1939 *Lepidodiscus fistulosus* Anderson: 68 (part).
1950 *Anglidiscus fistulosus* (Anderson) Regnéll: 6 (part).
1966 *Anglidiscus fistulosus* (Anderson) Regnéll: U162 (part).

Diagnosis. Agelacrinitid with a domal theca. Ambulacra tall, narrow; ambulacra I–III curve sinistrally, ambulacra IV and V curve dextrally. Cover plates arranged in an alternating series with both large and intercalated plates but precise arrangement not clear. Oral area markedly elongate. Oral cover plates small, undifferentiated from ambulacral cover plates; anterior and posterior series equally developed. Hydropore rise large, separated from oral area; includes one very prominent hydropore plate. Interambulacral plates numerous, squamose and imbricate. Anal pyramid narrow and prominently elevated. Peripheral skirt unknown.

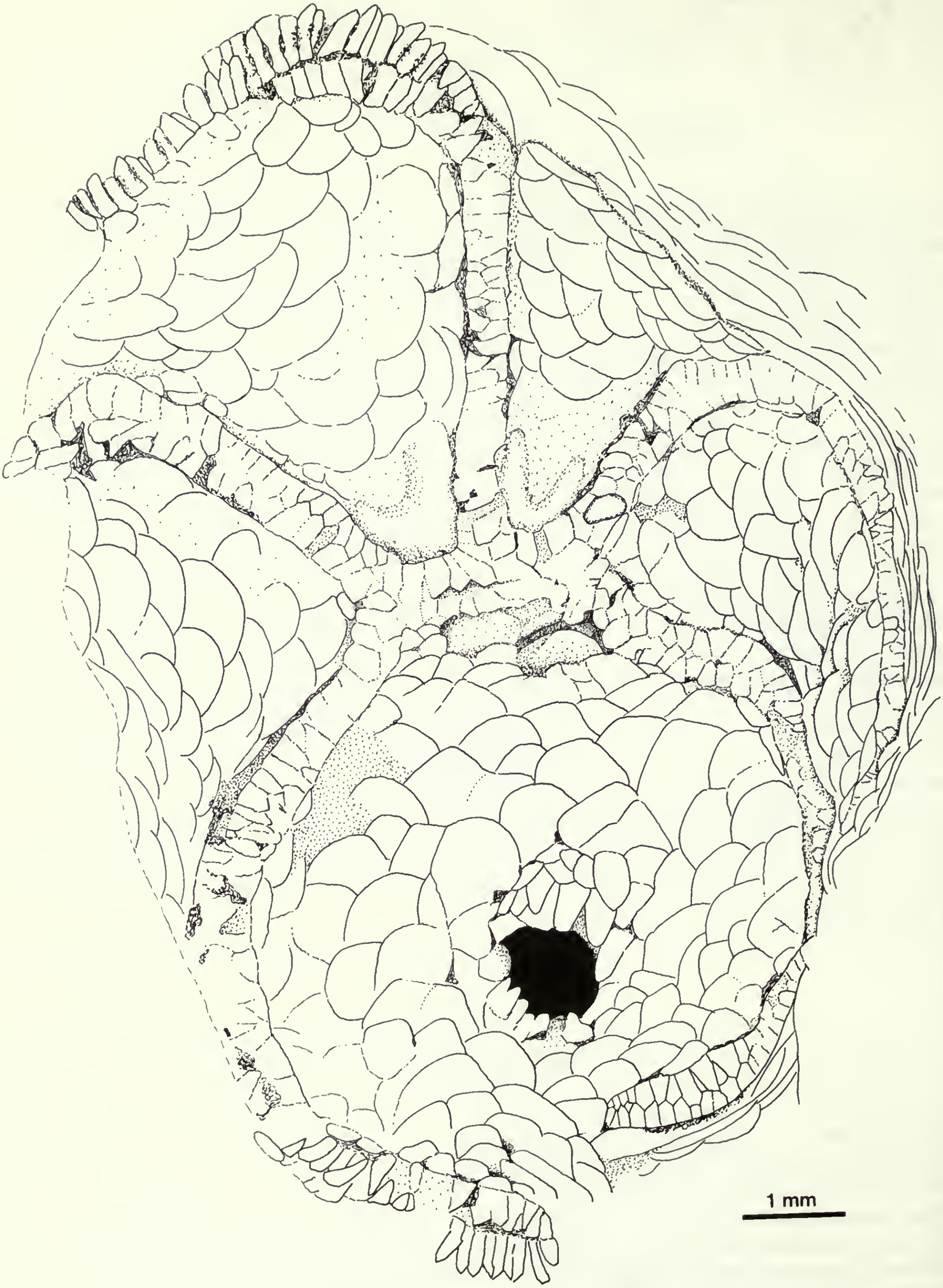


Fig. 11 *Postibulla neglecta* sp. nov. Camera-lucida drawing of the holotype, on IGS no. 60235 (P in Fig. 2). See Fig. 6.

NAME. 'Overlooked'.

MATERIAL. **Holotype**, Institute of Geological Sciences no. 60235, specimen xxvi of Anderson (1939: 70). Paratype, specimen xxx, same slab.

LOCATION AND AGE. Hetton House bore-hole, Northumberland (loc. iii, p. 114). Early Asbian, Dinantian.

DESCRIPTION. Both specimens are 12 to 13 mm in diameter and in life would have been moderately tall and domal in shape; they are preserved in their retracted state. Ambulacra are long and narrow and form prominent ridges over the theca. They are fairly straight adorally but towards the periphery they curve to run parallel with the margin. Ambulacra I–III curve sinistrally whereas ambulacra IV and V curve dextrally. The cover plates are tall and narrow. Where they have fallen outwards each can be seen to have a prominent sagittal ridge on its inner face. The cover plates form a tall steep-sided arch above the ambulacral grooves. Cover plate arrangement is not clear but there appears to be an irregular biseries of larger plates alternating with smaller intercalated plates (Fig. 11). The flooring plates cannot be seen.

The oral area is narrow but laterally extensive so that the ambulacra are in a clear 2–1–2 arrangement. The oral cover plates are continuous with ambulacral cover plates and there are no obviously larger plates. One large plate forms the posterior slope to the oral area opposite ambulacrum III but this I interpret as the most proximal interambulacral plate. An obvious mound to the posterior right-hand side of the oral area forms part of the hydropore structure. There is one large distal hydropore plate clearly separated from the oral area and a smaller proximal hydropore plate. Some of the proximal cover plates of ambulacrum V also border on the hydropore slit.

Interambulacral areas are formed of numerous squamous and imbricate plates. In the most adoral areas of interambulacra 2 and 3 there are crescentic raised areas (Fig. 6, p. 116) which Anderson (1939) interpreted, wrongly in my opinion, as the sites of gonads. The periproct is situated centrally in interambulacrum 5. It is narrow-based and composed of two cycles of rather elongate plates that are wedge-shaped in cross section. In the holotype the anal cone is preserved in its open position.

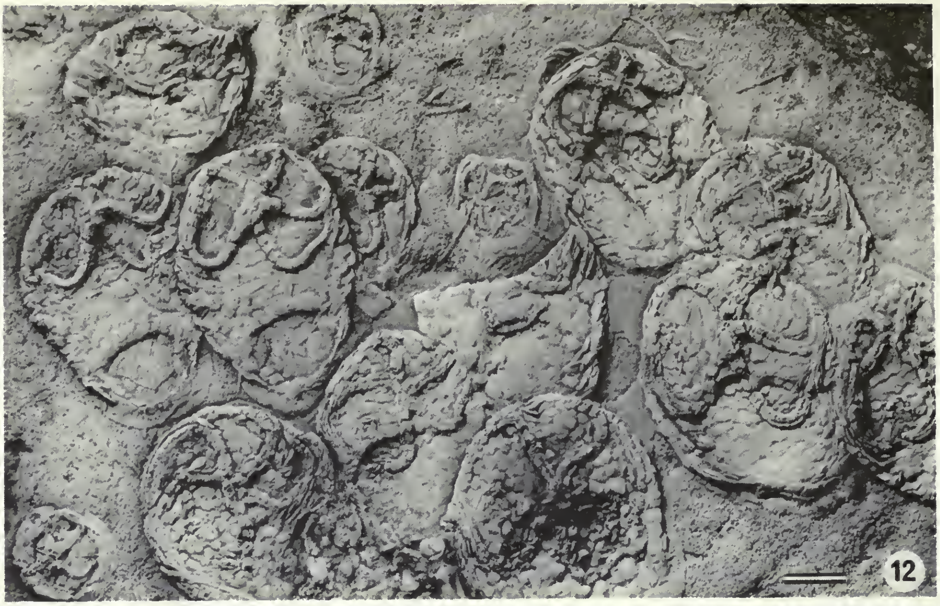
Beyond the ambulacra, interambulacral plates are vertical and stacked together, showing that the theca was tall in life and has since collapsed. Neither specimen shows the peripheral rim.

DISCUSSION. In erecting the species *Lepidodiscus fistulosus* Anderson (1939) did not realise that individuals belonging to two species (*Lepidodiscus* cf. *squamosus* and *Postibulla neglecta*) were present in his material. His composite reconstruction (1939: fig. 1) bears little resemblance to either species. The reconstruction of soft tissue anatomy given by Anderson (1939: fig. 6) is based on the internal appearance of the holotype of *Postibulla neglecta*. However, apart from the crescentic ridges adjacent to the oral area which he interpreted as the sites of gonads, other structural details cannot be verified.

Both the specimens are preserved upside down and reveal the mould of the external surface. As was discussed for *Lepidodiscus* cf. *squamosus* (p. 118) the specimens are not attached to a recognizable hard ground surface and were probably growing on fronds of a free-standing alga.

The arrangement of ambulacra, the steep-sided, narrow ambulacral ridges and the separation of the hydropore bulge from the oral area clearly place these specimens in the genus *Postibulla*. Five species of *Postibulla* are known, but only two of them come from the Carboniferous (Bell 1976*a*). These are *P. legrandensis* (Miller & Gurley) and ? *P. jasperensis* (Harker), both from the Kinderhookian, low in the Mississippian. *P. legrandensis* differs from the British species in having three plates forming the posterior rim of the hydropore opening and in having a prominent bulge directly opposite ambulacrum III on the posterior margin of the oral area (Bell 1976*a*: pl. 40). ? *P. jasperensis* is known only from one small specimen which was placed in this genus only with reservation by Bell (1976*a*). The cover plates are simple, not irregularly biserial, and the posterior oral proturberance is hardly developed; it is quite unlike the British specimens.

Postibulla neglecta is the youngest species of this genus known.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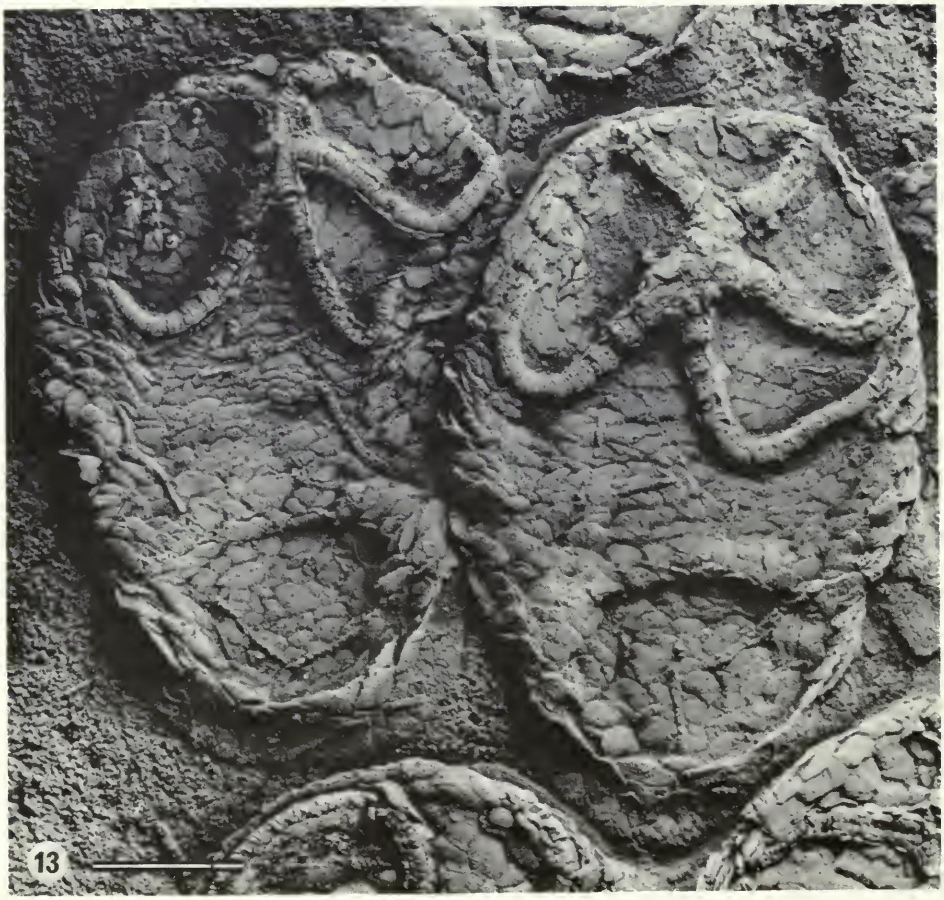
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Genus *STALTICODISCUS* nov.

Diagnosis. A genus of agelacrinitid with tall domal to subclavate theca. Ambulacra I–IV curve sinistrally, ambulacrum V curves dextrally. Ambulacral cover plates arranged in cycles of three, one of which is usually occluded adradially, and with an irregularly zigzag perradial suture. Hydropore rise included in posterior right of oral area (type VI of Kesling, 1960), posterior bounded by two or three plates only. Oral cover plates small, numerous, not differentiated from ambulacral cover plates. Flooring plates uniserial and strongly imbricate. Valvular anal cone consisting of two cycles of plates situated centrally in interambulacrum 5. Interambulacral plates more or less tesselate ventrally but becoming imbricate laterally where they form a cylindrical pedunculate zone. Peripheral skirt present, consisting of some five or six series of plates.

Name. Greek σταλτικός, 'contracting'.

Type species. *Lepidodiscus milleri* Sharman & Newton, 1892. Monotypic.

Distribution and age. From Penruddock, Cumbria and the River Irthing, Northumberland: Early Asbian.

Discussion. This genus is easily distinguished from *Lepidodiscus* on the arrangement of the cover plates. *Lepidodiscus* has cover plates that are arranged in cycles of six, usually with three larger plates and three smaller occluded plates (Fig. 10), whereas *Stalticodiscus* has cover plates arranged in cycles of three with two larger plates and a smaller, often occluded plate. *Discocystis*, like *Stalticodiscus*, has its cover plates arranged in cycles of three, or occasionally in cycles of four, but here the perradial edge of the cover plates is obviously serrated, suggesting that there are 'multiple intra-ambulacral extensions on the ambulacral tunnel surfaces of the cover plates' (Bell 1976*a*: 251). Furthermore, *Discocystis* has polygonal, tesselate plating in the interambulacral areas and a downwardly constricting pedunculate zone of subrectangular plates clearly demarcated from the ventral surface. In *Stalticodiscus*, interambulacral plating is, at most, sub-tesselate and the pedunculate zone is neither clearly demarcated from the ventral surface, not downwardly tapering. The flooring plates of *Discocystis* abut along vertical sutures, whereas those of *Stalticodiscus* are strongly imbricate. For these reasons *Stalticodiscus* and *Discocystis*, though clearly closely related, are separated as distinct genera.

Stalticodiscus milleri (Sharman & Newton, 1892)
Figs 12–51

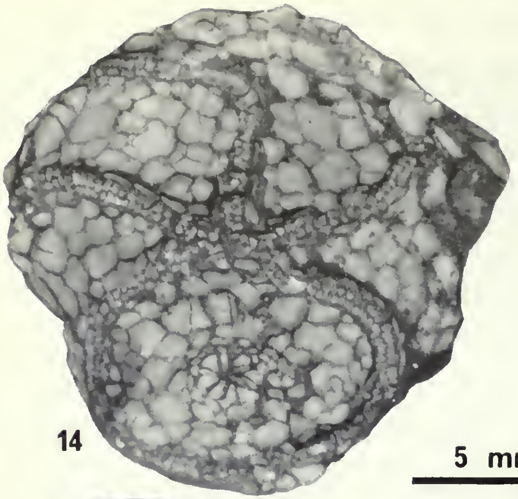
1892 *Lepidodiscus milleri* Sharman & Newton: 150; pl. 2, figs 1–5.
1936 *Lepidodiscus milleri* Sharman & Newton; Bassler: 20; pl. 7, fig. 7.

Diagnosis. A subclavate species of *Stalticodiscus* up to 15 mm in diameter and 30 mm or so in height. Interambulacral plating sub-tesselate ventrally, imbricate laterally. Periproct situated centrally in interambulacrum 5. Ambulacra I and V just overlapping behind the periproct in adults.

Material. Holotype, Institute of Geological Sciences no. 7662. Other specimens, IGS 25105, also many hundreds of individuals from Penruddock, British Museum (Natural History) Palaeontology Dept nos E29878–925.

Location and age. The holotype IGS 7662 and IGS 25105 come from the Millerhill limestone, Early Asbian, of the River Irthing, Northumberland. The holotype comes from near Waterhead

Figs 12–13 *Stalticodiscus milleri* (Sharman & Newton), BM(NH) no. E29878. Fig. 12, a limestone concretion encrusted by adults some in extended posture. Notice that all are aligned with their anterior towards the right or top right. Fig. 13, an enlarged view of the two fully extended individuals seen in Fig. 12, showing the imbricate pedunculate zone. On collapse the theca has been compressed onto its own elevated peripheral rim to produce the circular impression towards the base. Scale bar = 5 mm. All specimens whitened with ammonium chloride sublimate.



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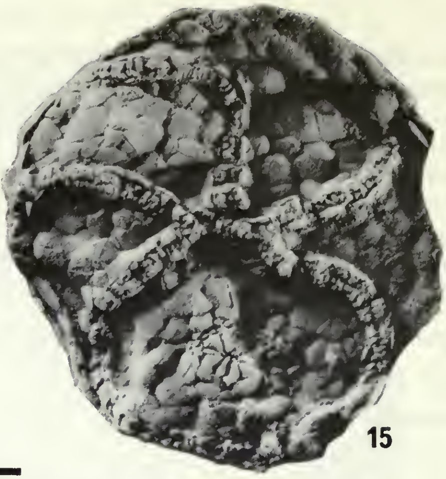

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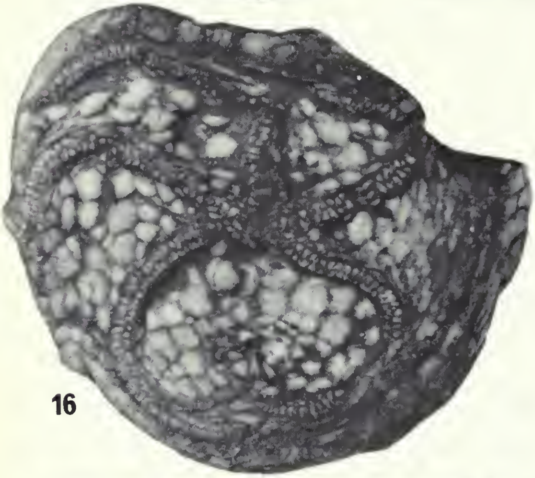

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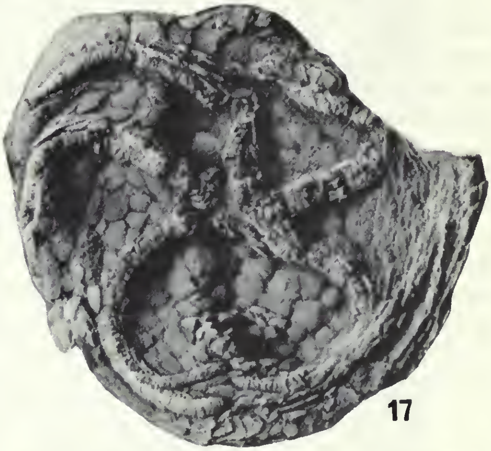

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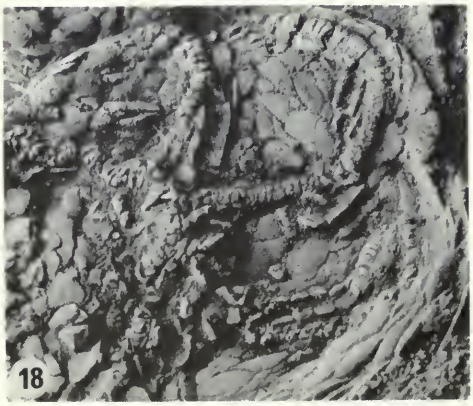

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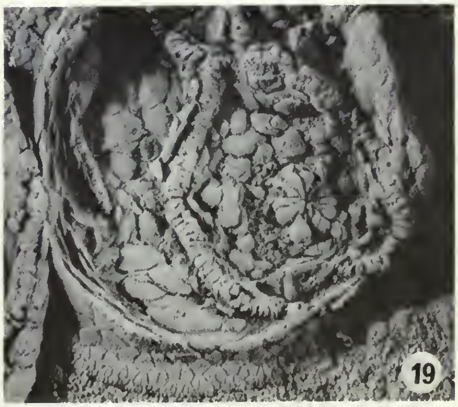

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Figs 14–19 *Stalticodiscus milleri* (Sharman & Newton). Figs 14–15, BM(NH) no. E29884: Fig. 14 under xylene, Fig. 15 whitened with ammonium chloride sublimate. Figs 16–17, BM(NH) no. E29889: Fig. 16 under xylene, Fig. 17 whitened with ammonium chloride sublimate. Fig. 18, BM(NH) no. E29885. Oral surface with cover plates partially lost to reveal uniserial flooring plate arrangement. Fig. 19, BM(NH) no. 29888. Posterior half of the specimen showing the peripheral rim plating and the arrangement of plates forming the periproct. Note the large hydropore bulge to the posterior right of the oral area. Scale bar 5 mm.

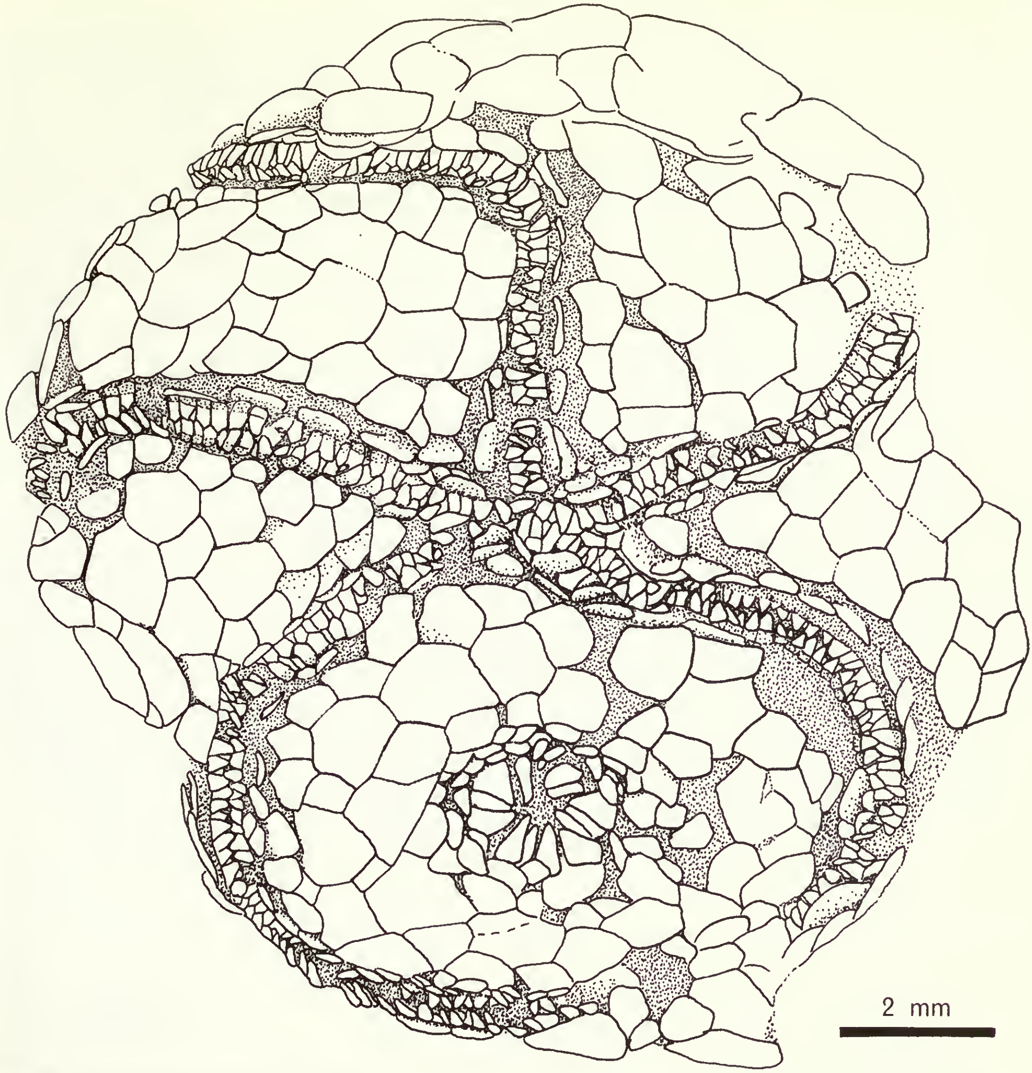


Fig. 20 *Stalticodiscus milleri* (Sharman & Newton), BM(NH) no. E29884. Camera-lucida drawing.

(loc. i, p. 114), the other from near Lampert (loc. ii). Many hundreds of individuals encrusting limestone concretions have also been collected from Penruddock, Cumbria (loc. v) and are also Early Asbian in age.

Description. Until recently, only two poorly-preserved specimens of this species were known. The discovery of colonies totalling many hundreds of individuals, ranging in size from less than 0·5 mm to more than 15 mm in diameter, at Penruddock has provided an abundance of well-preserved material on which to base this description.

Mature individuals are subclavate in shape when fully extended (Fig. 13) but are usually preserved in a contracted posture with the lateral peduncular zone telescoped together just inside the marginal ring (Fig. 27). When fully extended the theca is twice as tall as it is broad, and it tapers slightly towards its attachment base. The ambulacra extend down less than half the height of the theca. Juveniles are less elevated and generally domal in shape. The pedunculate zone only starts to become obviously developed once individuals have reached a diameter of about 8 to 10 mm. The peripheral rim is usually circular in outline but may be distorted if the individual is attached to an uneven surface or a relatively small object such as a shell.

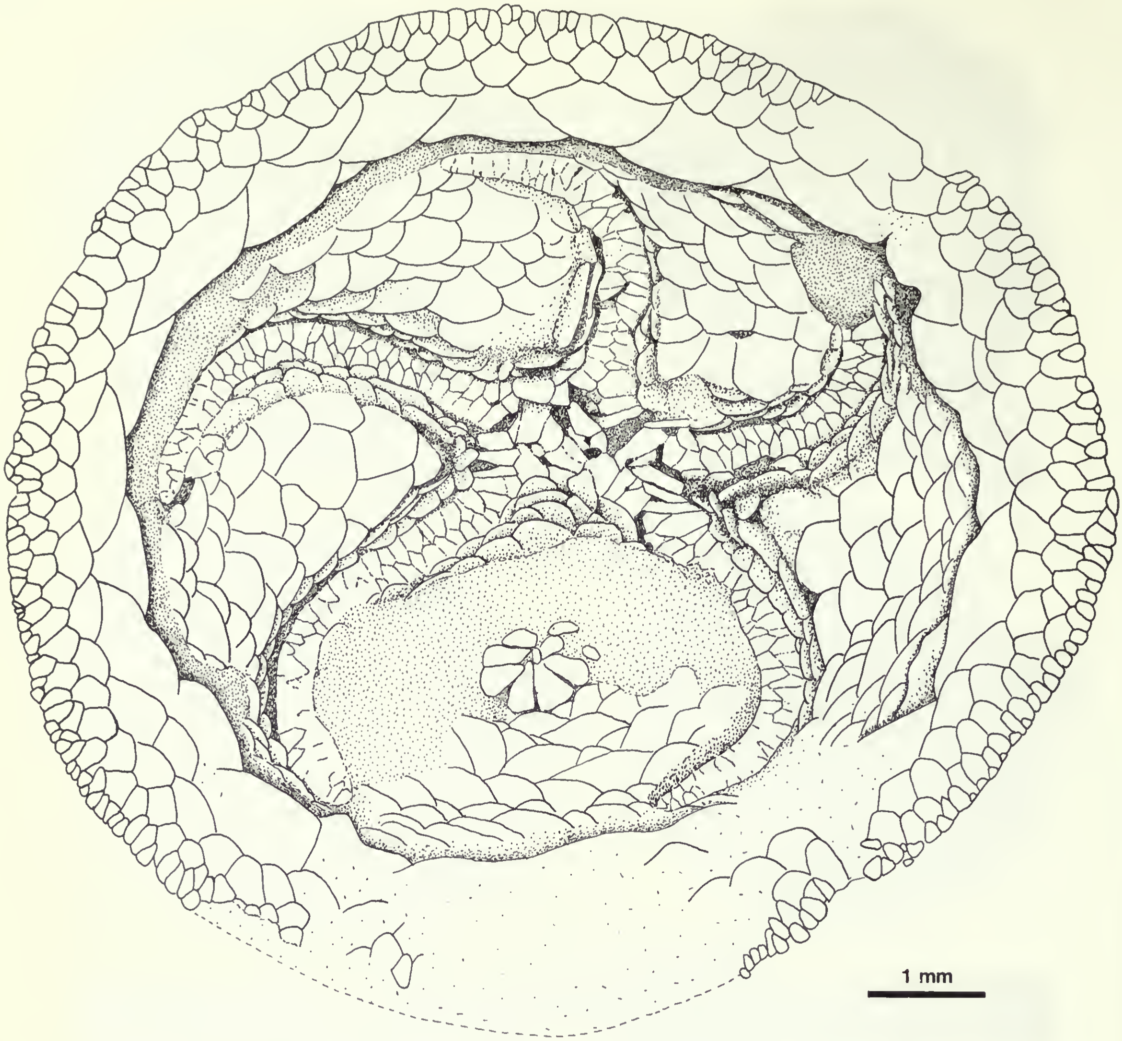
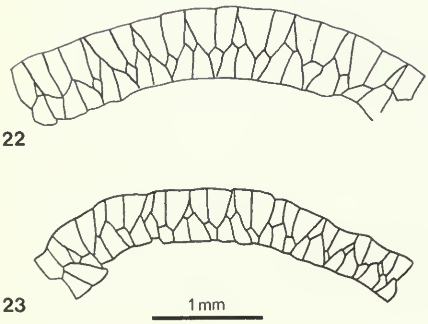


Fig. 21 *Stalticodiscus milleri* (Sharman & Newton), IGS no. 7662, holotype. Camera-lucida drawing. See Fig. 25.



Figs 22–23 Camera-lucida drawings of ambulacral cover plate arrangement in *Stalticodiscus milleri* (Sharman & Newton), approximately mid-length along the ambulacrum. Fig. 22 BM(NH) no. E29571; Fig. 23 BM(NH) no. E29885.

Ambulacra form prominent ridges over the theca, and are only moderately long. Ambulacra I–IV curve sinistrally, ambulacrum V curves dextrally. The two posterior ambulacra curve round to encircle the periproct, but it is only in the largest individuals that the two ambulacra more or less meet posteriorly behind the periproct. These ambulacra may just overlap at the anterior–posterior mid-line. Ambulacra maintain a uniform breadth along most of their length, tapering only at their distal tip. Cover plates are arranged in irregular cycles of three, usually consisting of two larger plates and a smaller, often occluded plate (Figs 22, 23). Proximally, near the oral area plating becomes more irregular. Near the distal tip (Fig. 34) the perradial suture is obviously zigzagged, but over most of the ambulacrum this suture is much more irregular in its path (Fig. 30, p. 131).

Cover plate arrangement continues across the oral area without obvious distinction from ambulacral areas (Figs 30–32). A few plates are slightly larger than any found in the ambulacra, but there are no enlarged primary oral plates. Two shared cover plates situated at the fork between paired lateral ambulacra are usually conspicuous. The arrangement of plates in the oral area is not fixed, and in the large number of specimens available much variation exists, particularly in the presence or absence of small occluded plates.

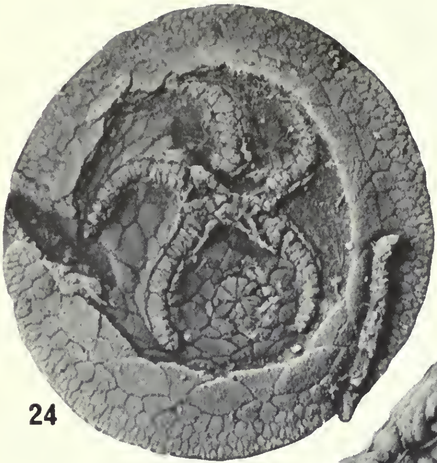
Ambulacral flooring plates are uniserial and imbricate. Each plate has a large distal tongue which overlaps the base of the adjacent flooring plate (Figs 38–40). This imbrication is not immediately apparent from an external view of an ambulacrum stripped of its cover plates (Fig. 18). Flooring plates have a deep, U-shaped channel which shows no signs of muscle attachment scars or grooves for soft-tissue tracts. Although the floor of this channel is relatively thick, the lateral walls are thinner. There is a distinct bulge on each side approximately half-way along (Figs 38–40). The functional significance of this structure is unknown but it is present in at least some other agelacrinitid edrioasteroids (Bell 1976*a*). Cover plates rest on top of the lateral walls of the flooring plates but there appears to be no obvious structural modification to accommodate them. Adradially the cover plates have a small intrathecal extension which overlaps the flooring plate to extend beneath adjacent interambulacral plating (exposed in areas shown in Figs 31 and 34). The structure of the oral frame is unknown but is presumably like that of other agelacrinitids.

The hydropore structure forms a distinct bulge to the right posterior of the oral area (Figs 27–31). It is bounded by several cover plates of ambulacrum V anteriorly and by two large hydropore plates to the posterior. The hydropore bulge matches a type VI hydropore of Kesling (1960).

Interambulacral areas are broad. On the ventral surface the plating is sub-tesselate (Figs 14–17) but laterally the interambulacral plates imbricate to form a pedunculate zone. Interambulacral plates are thin with bevelled edges. The outer surface is covered by a dense stereom layer with a granular surface (Figs 31–36). The bulk of the plate is thickened with a coarse labyrinthic stereom but there are a couple of retiform stereom layers near the outer surface (Figs 37, 41). Within each interambulacrum larger plates are found towards the centre whereas smaller plates border the ambulacra and surround the periproct. The imbricate plating making up the pedunculate zone is arranged irregularly (Fig. 13). This zone could be expanded and contracted like a telescope by varying the amount of overlap of the constituent plates. Presumably there were both meridional and circumferential muscle layers underlying the thecal plating to bring about this change in shape.

The periproct lies centrally in the posterior interambulacrum. It forms a well-defined anal cone composed of two cycles of plates. The primary cycle consists of some eight large triangular plates. Within this cycle, and largely hidden from sight, is a second cycle of smaller plates lying distally nestled between primary anal cone plates. When the anal cone is undisrupted only the very tips of these secondary plates can be seen at the apex of the cone (Fig. 30). In large specimens the primary and secondary plates alternate.

The peripheral rim is circular in outline and forms a cohesive framework. It consists of some five rows of plates which become progressively smaller towards the margin (Figs 19, 24, 36). The innermost plates alternate, every other plate being set behind. These plates have an expanded base which is set firmly on the substratum. The base is marked by a series of radial ridges and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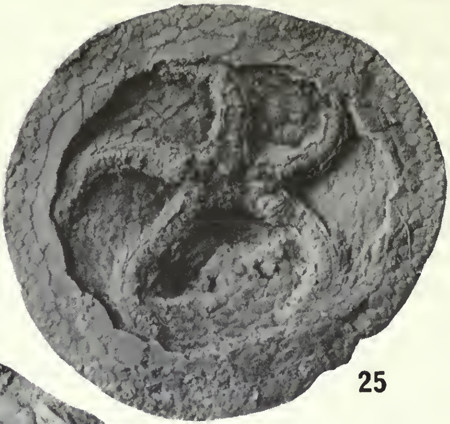
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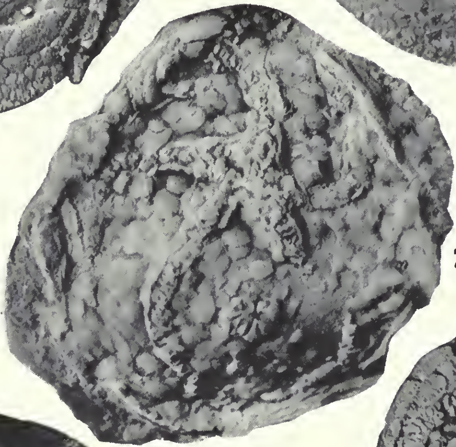
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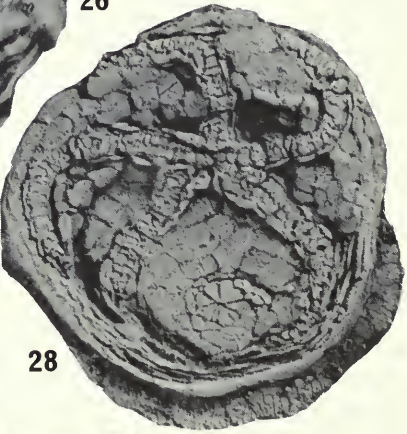
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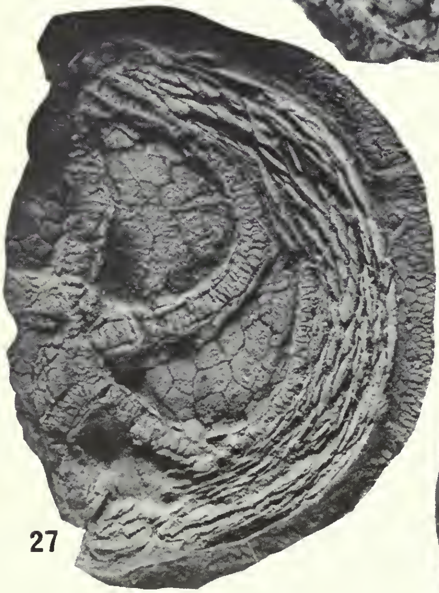
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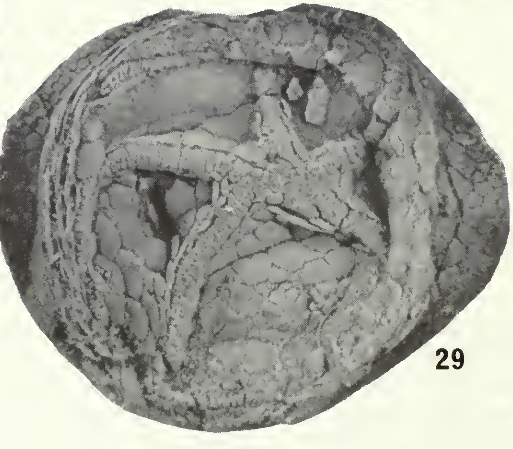
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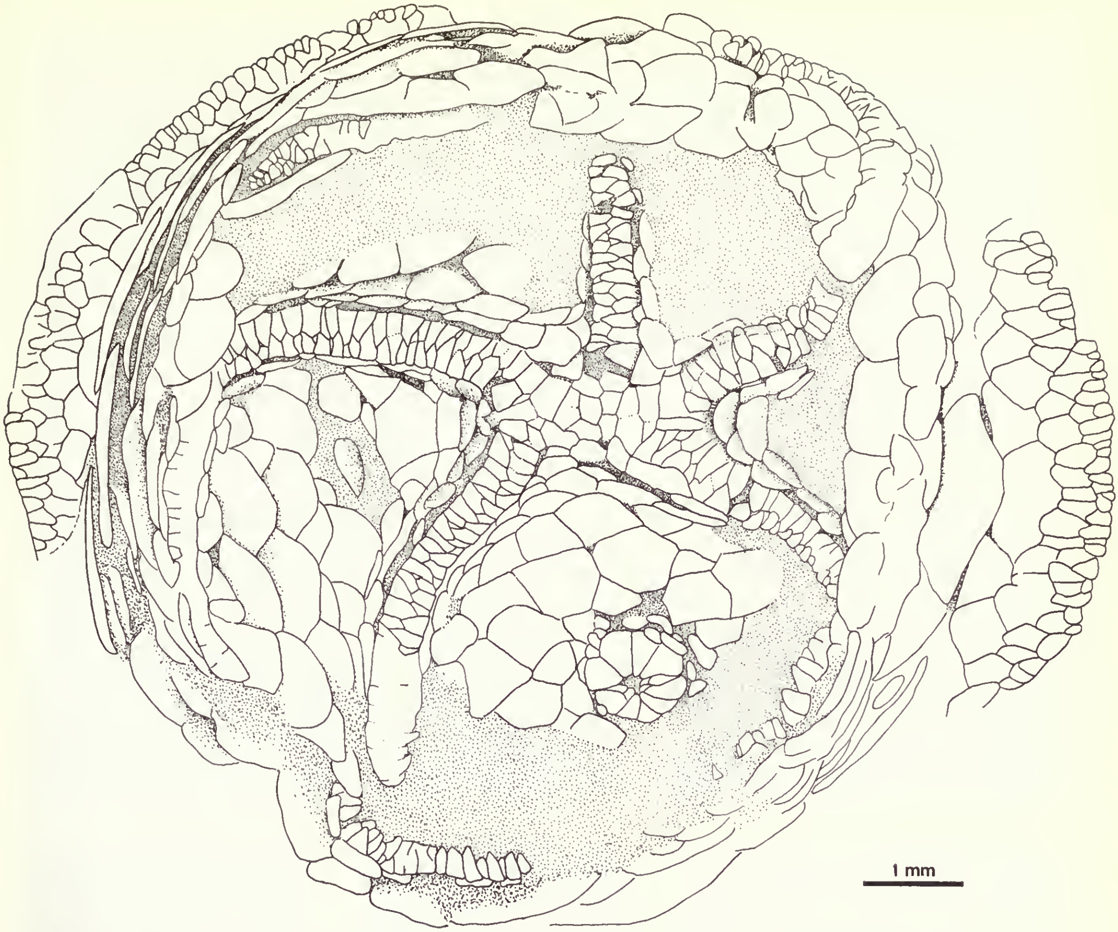
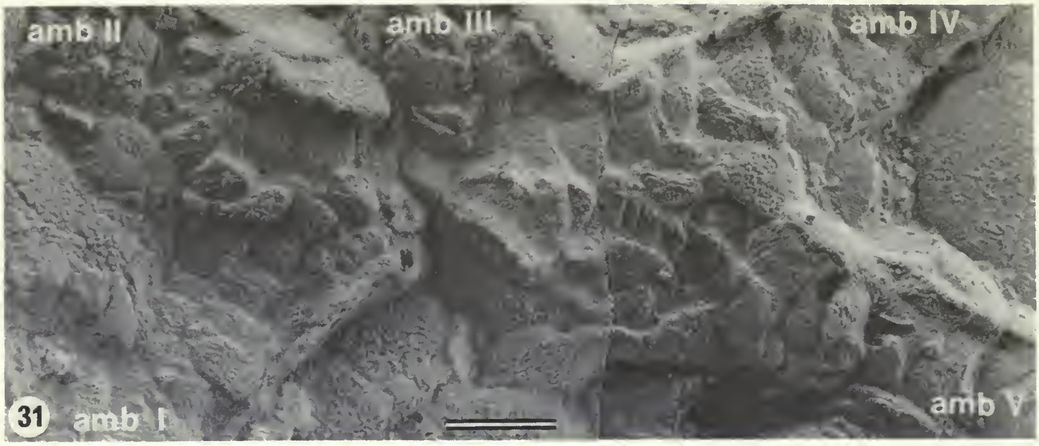


Fig. 30 *Stalticodiscus milleri* (Sharman & Newton), BM(NH) no. E29887. Camera-lucida drawing showing the cover plate arrangement in the oral area. See Fig. 29.

grooves which presumably played some role in adhesion. The more distal plates of the peripheral rim are tesselate and also have radial ridges on their lower surfaces, but these are less well developed.

GROWTH. The changes that take place during the growth of isorophid edrioasteriods have been described by Bell (1976*b*). Bell was able to study ontogeny in all the isorophid families save for the Agelacrinitidae. The large number of juvenile *Stalticodiscus milleri* now available permits the first detailed description of growth in a member of the Agelacrinitidae. In this study, small individuals were studied using a scanning electron microscope and a representative growth series is shown in Figs 42–51.

Figs 24–29 *Stalticodiscus milleri* (Sharman & Newton). Fig. 24, BM(NH) no. E29886, 7 mm diameter juvenile, ×8. Fig. 25, IGS no. 7662, holotype from the River Irthing, ×6; see Fig. 21. Fig. 26, IGS no. 25105, the other specimen mentioned by Sharman & Newton (1892) as coming from the River Irthing, ×6. Fig. 27, BM(NH) no. E29879, a large specimen; anterior to the right showing the well-developed zone of imbricate plates, ×6. Fig. 28, BM(NH) no. E29883, small adult from Penruddock with the same diameter as the holotype, ×6. Fig. 29, BM(NH) no. E29887, specimen with a well-preserved oral area, ×6; see Fig. 30. All specimens whitened with ammonium chloride sublimate.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amb II
amb III
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amb V
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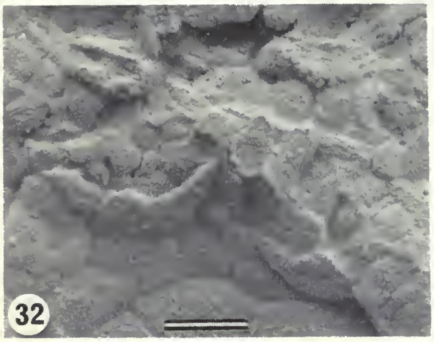
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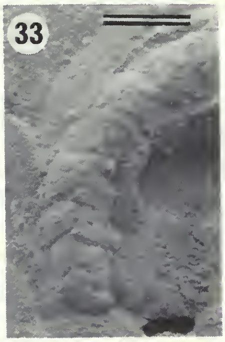
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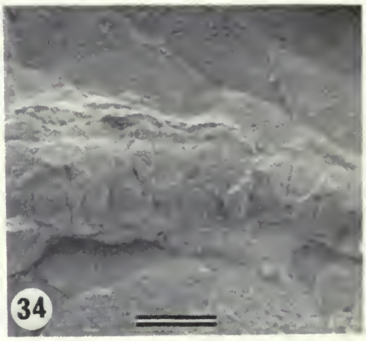
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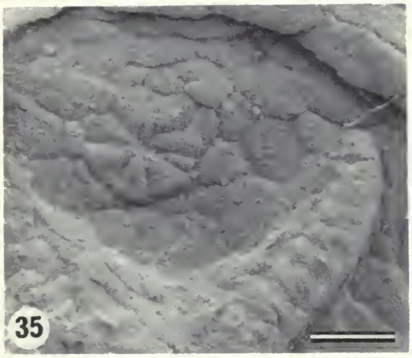
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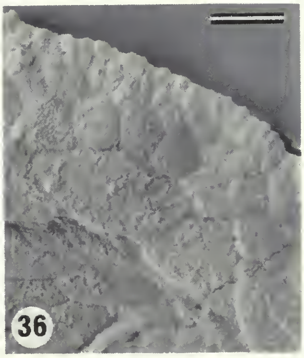
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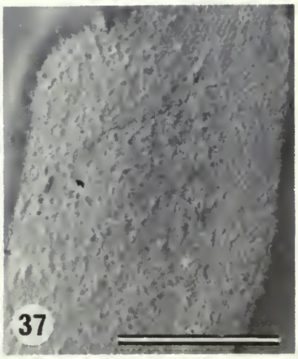
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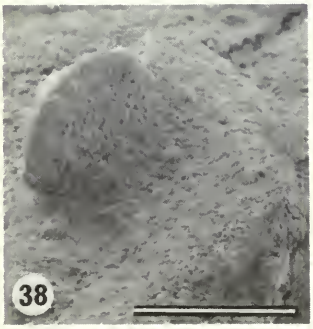
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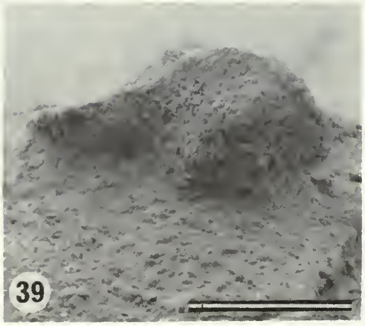
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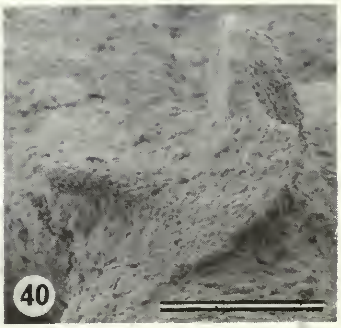
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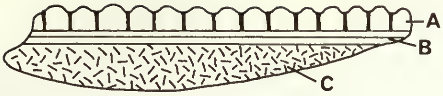
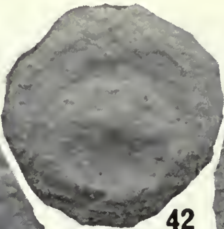


Fig. 41 Reconstructed cross section through an interambulacral plate of *Stalticodiscus milleri* (Sharman & Newton). A, outer dense, perforate stereom layer with granular surface. B, thin middle layer of laminar stereom. C, thick inner layer of coarse labyrinthic stereom.

As in all isorophids, the peripheral rim is much more prominent in juveniles than it is in adults. The central disc is only 55% of the diameter of the theca at about 1 mm diameter, approximately 60% at 2–3 mm diameter, 65–70% at 4–7 mm diameter and reaches a little less than 80% by 12–15 mm diameter. At 1 mm diameter the peripheral rim consists of just two rows of plates but the number of rows increases progressively to a total of five by about 7–8 mm diameter (Fig. 36). Bell (1976*b*) reported that new peripheral rim plate cycles were added by insertion between the first two cycles of plates. I could find no evidence that this took place in *S. milleri*, where new plate cycles appear to have been added at the outer edge. The inner alternating cycle of large peripheral rim plates do not form an obvious palisade until about 2 mm diameter. New plates continue to be added to the inner cycle of plates until approximately 6 mm diameter, after which time growth continues by plate enlargement only.

Within the disc, plating is poorly differentiated to start with. At 1 mm diameter the disc is dominated by an elongate mound (Fig. 42) but at this size it is impossible to distinguish individual plates. Presumably at this stage ambulacral cover plates exist but are extremely thin and poorly preserved. By 2 mm diameter the ambulacra have started to differentiate and there are five small but distinct points to the elongate oral area. Cover plate arrangement can be made out and there are four slightly larger cover plates in the oral area; two anterior ones situated at the junction of ambulacra II and III, and ambulacra III and IV, and two posterior ones between ambulacra I and V. The large posterior right oral cover plate eventually becomes the hydropore plate. At 2 mm diameter the rudimentary ambulacra consist of just two or three cover plates per column, but by 4 mm diameter the ambulacra are obviously developed and consist of some six to eight cover plates per column. Ambulacra are still more or less straight. The ambulacra start to curve gently by about 5·5 mm diameter (by which time there are 12 to 14 cover plates per column) and, for the first time, small occluded cover plates become apparent. The cyclical arrangement of cover plates is fully developed by 7 or 9 mm diameter. At 7 mm diameter the anterior and two lateral ambulacra are more or less prominently curved, but the posterior two ambulacra are only weakly curved and their tips only slightly convergent. By 13 mm diameter the posterior two ambulacra have grown to more or less meet behind the periproct and in larger specimens the tips of the ambulacra may overlap very slightly. New ambulacral cover plates are added distally at the tips of growing ambulacra.

Figs 31–40 Scanning electron micrographs of *Stalticodiscus milleri* (Sharman & Newton) from Penruddock. All BM(NH) numbers. Fig. 31, E29907, oral area of a 13 mm diameter individual showing a clear hydropore bulge. Fig. 32, E29908, individual 10 mm in diameter showing a rather different arrangement of oral cover plates. Fig. 33, E29915, the distal part of ambulacrum II in an 8 mm diameter individual, showing the early appearance of secondary (occluded) cover plates near the distal tip. Fig. 34, E29908, the adoral part of ambulacrum V in a 10 mm diameter specimen showing the cyclical arrangement of cover plates and the zigzag perradial suture. Fig. 35, E29897, periproct in a 5·5 mm diameter individual with both primary and secondary cycles of periproctal plates; see Fig. 51. Fig. 36, E29895, the fully formed peripheral rim of plates in an individual 6·5 mm in diameter. Fig. 37, E29921, a large interambulacral plate seen from the inside with an extensive zone of labyrinthic stereom and a more marginal laminar stereom. Figs 38–40, E29918, ambulacral flooring plate: Fig. 38, external (distal edge to top of photomicrograph); Fig. 39, lateral (distal edge to left of photomicrograph); Fig. 40, front view of distal face. Scale bar = 0·5 mm.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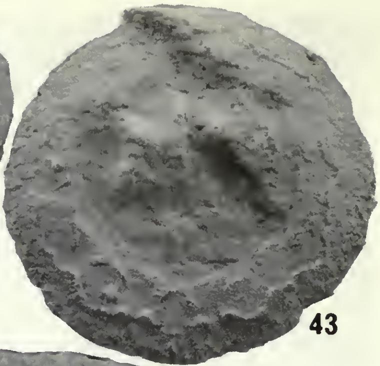
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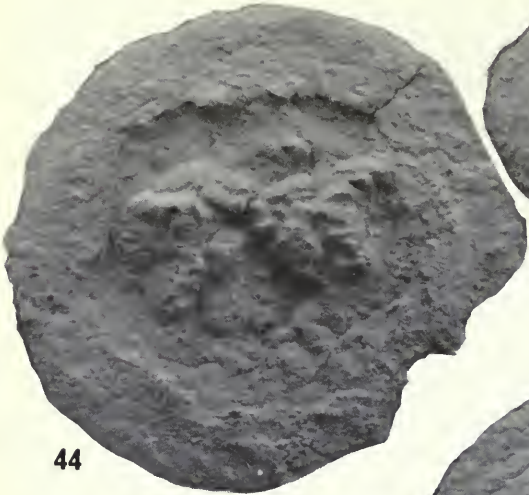
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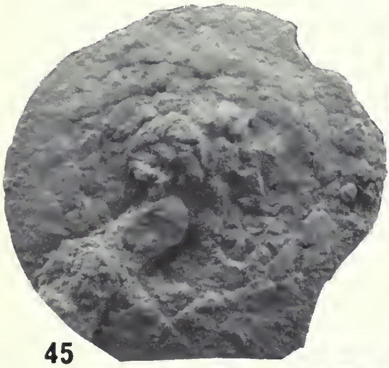
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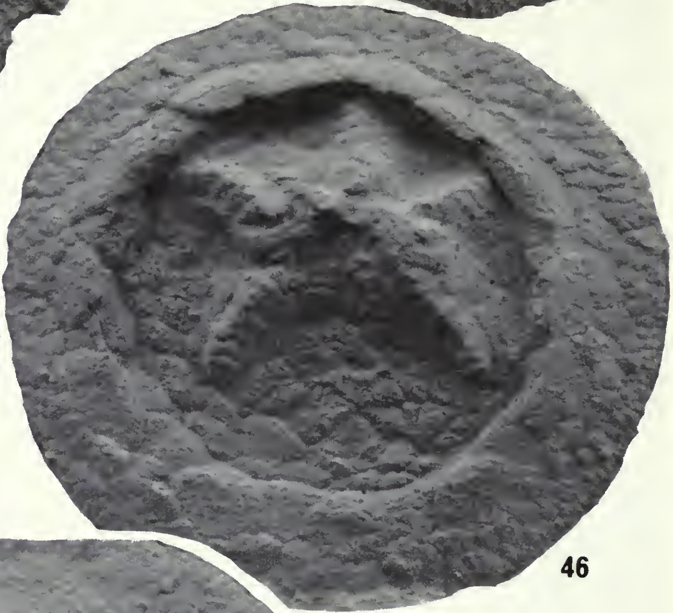
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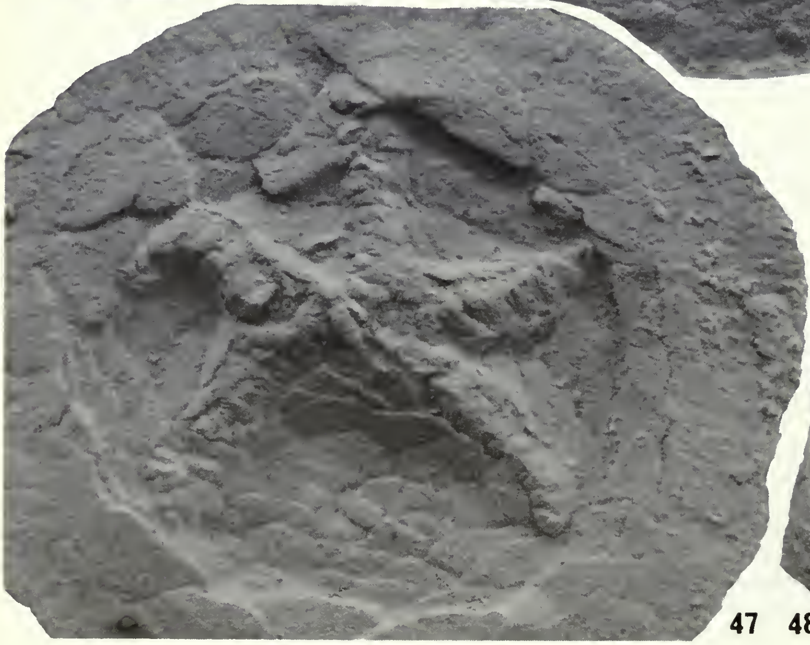
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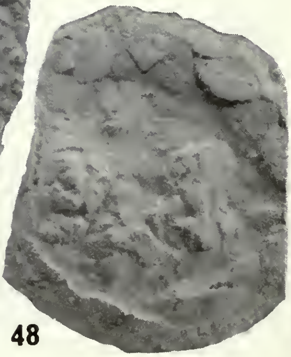
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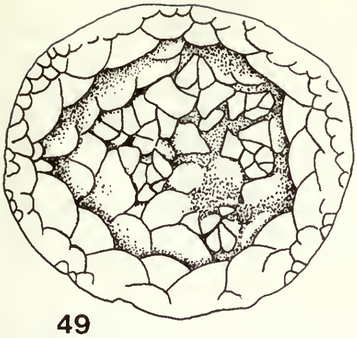

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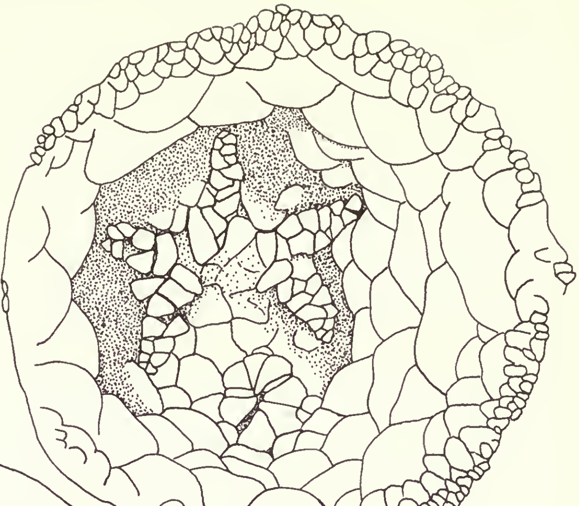

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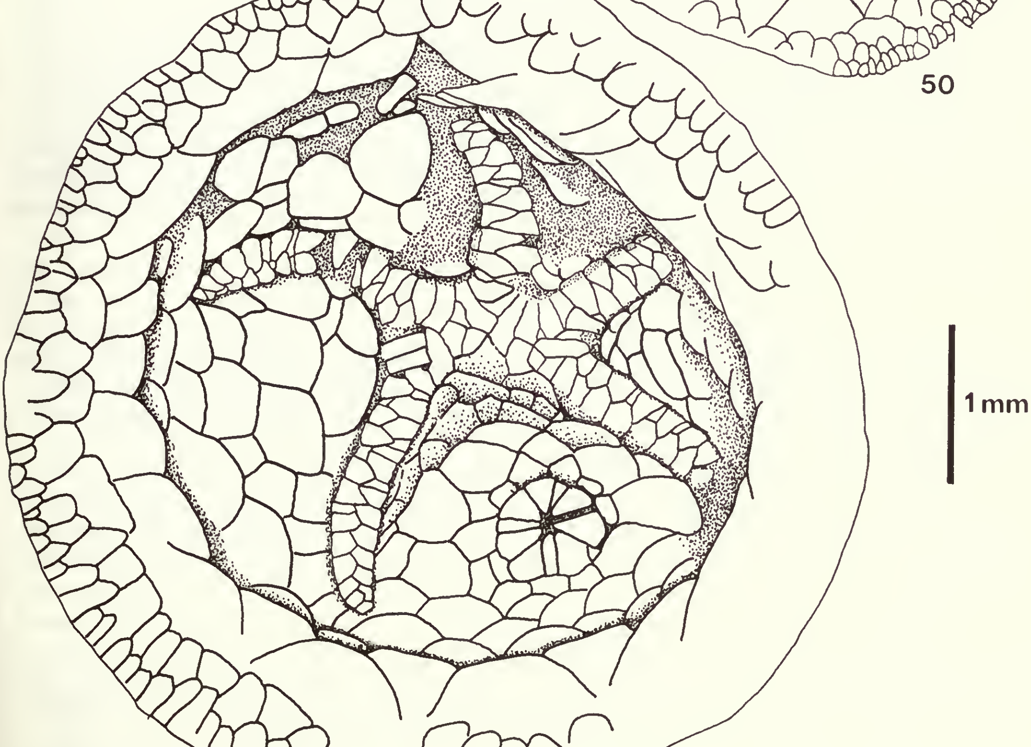

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Figs 49–51 Camera-lucida drawings of juvenile *Stalticodiscus milleri* (Sharman & Newton). All BM(NH) numbers. Fig. 49, E29893, see Fig. 48; Fig. 50, E29885; Fig. 51, E29897, shown inverted in Fig. 35, p. 132.

Figs 42–48 Scanning electron micrographs of juvenile *Stalticodiscus milleri* (Sharman & Newton), all to the same scale. All BM(NH) numbers. Fig. 42, E29899; Fig. 43, E29898; Fig. 44, E29911; Fig. 45, E29917; Fig. 46, E29901; Fig. 47, E29894; Fig. 48, E29893, see Fig. 49.

Interambulacral areas are minimal at 1 mm diameter and no interambulacral plates can be made out at this size. Interambulacral plates first become apparent at about 2 mm diameter. As growth proceeds, interambulacral areas become progressively larger relative to the disc, and new plates are added immediately inside the peripheral rim as well as adjacent to the ambulacra and periproct. By about 8 mm diameter the full complement of ventral interambulacral plates are present and it is at about this size that the pedunculate zone starts to develop. At 7 mm diameter the theca is still low and domal in profile but around 8 to 10 mm diameter a zone of imbricate plating starts to form between the edge of the ventral surface and the peripheral rim. This pedunculate zone is fully developed by 12 to 15 mm diameter, but at what stage it starts to develop varies. For example, it is poorly developed in the holotype, which is 9 mm in diameter, but most Penruddock specimens have a fairly well developed zone of imbricate plates by this diameter. Presumably environmental factors influenced the size at which the pedunculate zone formed.

The periproct does not appear until about 2 mm diameter, at which stage it is a circular area composed of some four triangular plates set flush with the interambulacral plates. By 3 mm diameter the periproct has become elevated and forms a conical structure, and by 4 mm diameter the full complement of primary cycle periproctal plates is present. At about 6 mm diameter the first of the secondary cycle of periproctal plates appears.

Plating arrangement over the oral area is in its final form by about 6 mm diameter. The hydropore cover plate appears very early and is present by 2 mm diameter. It continues to enlarge throughout the early growth stages. The hydropore bulge to the posterior right of the oral area is absent at 4 mm diameter, starts to form at about 5 to 6 mm diameter and is prominent by 7 mm diameter. This probably coincides with the onset of gonadal development, as the so-called hydropore passageway is probably a combined hydropore/gonopore. The appearance of the hydropore bulge would then be the best morphological change on which to distinguish juveniles from sexually mature adults.

The ontogenetic changes that take place in *S. milleri* are in close agreement with the development of other isorophids reported by Bell (1976*b*). There are, however, two minor differences. Firstly, I could find no evidence that plates of the peripheral rim were added by insertion: here addition took place at the outer edge. Secondly, the cover plates of the oral area are hardly differentiated from ambulacral cover plates even during the early ontogenetic stages. This quite obviously reflects the fact that in adult agelacrinitids there are no enlarged oral cover plates such as are found in other families.

DISCUSSION. The holotype of '*Lepidodiscus*' *milleri* is not well preserved and comes from a slightly higher horizon in the Early Asbian than does the Penruddock material. The holotype differs slightly from the Penruddock material in that it has a more juvenile appearance than would be expected for its size. At 9 mm diameter it has the appearance of a 7 mm diameter Penruddock specimen, lacking the pedunculate zone development and strong ambulacral curvature expected by this size. As the only difference between the holotype and the Penruddock specimens is one of developmental rate, all are placed within the same species. The rate of ontogenetic development is likely to be influenced by environmental factors such as the hydrodynamic regime or substratum availability and intraspecific competition.

The Penruddock population of *S. milleri* was killed by a sudden influx of sediment and the animals are preserved in various stages of contraction (compare Figs 13 and 27). Specimens that are not fully contracted are generally preserved lying over to one side (see, for example, Fig. 12), flattened by the influx of sediment that killed them. The direction in which they have fallen presumably coincides with the prevailing current direction at death. The fully contracted specimens have collapsed further following compaction and probably had a low domal profile in life. Presumably contraction and expansion were effected by circumferential and longitudinal muscle layers immediately beneath the thecal plating. Adults were not permanently cemented to the substratum but could swivel, much like sea anemones. Orientation is more or less random on boulders settled by juveniles. However, once the pedunculate zone had begun to form, orientation obviously became more important. For example, on BM(NH) nos E29878–82 (one

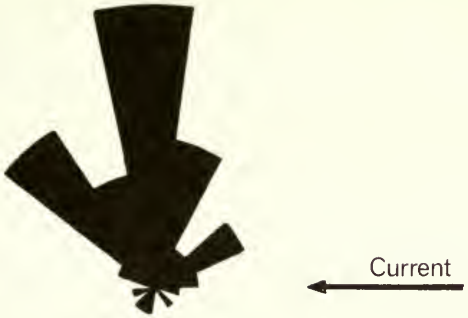

Fig. 52 Rose diagram showing the orientation (anterior of the anterior–posterior axis) for 55 adults encrusting one limestone concretion. The current arrow shows the direction in which the sediment that smothered the colony was brought in.

boulder), all adults are orientated in the same direction with their anterior ambulacra facing more or less at right angles to the direction of sediment input that killed them (Fig. 12). A strong orientation is found on many other boulders (Fig. 52), though not on all. The direction of sediment input need not correspond to the direction of the prevailing current. However, Foerste (1914) found precisely the same orientation in populations of *Carneyella pilea*. Here, as in *S. milleri*, it is ambulacra IV and V that face towards the direction of sediment influx. The fact that in both species the anteior–posterior axis was orientated at right angles to the direction of the current that smoothered them suggests that this was indeed the orientation that they adopted in currents. It also suggests that these isorophids were living in a tidal regime with bimodal currents, since in unidirectional flow one would expect the anterior to face into the current so that the periproct was positioned downstream of the mouth.

Acknowledgements

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A survey of Recent and fossil Cicadas (Insecta, Hemiptera–Homoptera) in Britain

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Synopsis

The current status and origin of the single extant British cicada, *Cicadetta montana* Scopoli, are discussed. An account of cicadas from the Tertiary and Mesozoic of Britain is given with an analysis of the taxonomy and morphology of the Mesozoic species. The family Cicadidae is recorded from the Mesozoic for the first time.

Introduction

This survey was prompted by an examination of specimens of cicadas amongst the British Upper Triassic collections at the Institute of Geological Sciences and the British Museum (Natural History).

Rohdendorf (1962) divided the 'infraorder Cicadomorpha' into two superfamilies, Palaeontinidea and Cicadidea. In the latter he placed three families, Prosbolidae, Cicadidae and Tettigarctidae. The Prosbolidae are known only from the Carboniferous to Triassic (Evans 1956: 196–206). The Cicadidae, which include the only British species, *Cicadetta montana* Scopoli, are widespread in the warmer parts of the world (Evans 1963) but extend into the temperate zone where they are represented by fewer species. As fossils the Cicadidae are known from the Tertiary, Zherikhin (1980) suggesting the Upper Cretaceous as the earliest record. The Tettigarctidae are common in the fossil record since the early Mesozoic and occur in the Tertiary. In contrast with the widespread distribution and numerous species of Recent Cicadidae, the only two living species of Tettigarctidae are restricted to Australia.

Recent cicadas in Britain

Cicadetta montana in Britain is restricted to a very small area in Hampshire (Grant 1972). Morley (1941) gave an account of the history and distribution of *C. montana*, stating that it has been 'in our midst since Britain's severance from the continent in Pliocene times'. He also pointed out that with its limited powers of flight it could not cross the Channel, although it is found in northern France (Villiers 1977). Grant (1972) supported the view that *C. montana* is a relict species, stating that its history in Britain 'is directly traceable to the old land continuity with Europe and ancient vegetative spread'. It is evident from recent work (Grant 1970, 1972; Morley 1941) that *C. montana* has never been a common insect and is mostly restricted to one southern county. It is not an easy insect to locate in the woods, in spite of its call, and it has been suggested that this call is inaudible to some people (Morley 1941: 54).

C. montana was first discovered in Britain in 1812 but Curtis (1832) commented that he and another well-known entomologist (Dale) searched for it without success for over 20 years before they finally rediscovered it. Buckton (1890) in his monograph on British Homoptera also commented on its local and very patchy occurrence. Both Grant and Morley dismissed as unlikely natural or accidental introduction of the cicada to Britain because of its relatively weak powers of flight, ephemeral adult life and subterranean early stages. However, the eggs of the cicada, which are inserted into the stems of woody plants, might well have been brought (accidentally) into Britain. A modern parallel can be drawn from the homopteran

Graphocephala fennahi Young which was first recorded in Britain in 1936 as an introduction (under the name *C. coccinea* Forster). This species lays its eggs in the sepals of rhododendron (Morcos 1953).

Morley's (1941) suggestion of the Pliocene for the origin of the British cicadas is unacceptable since it implies that this warm-loving species had survived several glacial periods in Britain. Grant's (1972) suggestion of an origin during the Boreal age (Flandrian, *c.* 7000 years B.P.) is more plausible, but I believe that if cicadas were present prior to the early 1800s then some folk-lore or published account of this large and relatively noisy insect would have appeared. However, if the 'little ice-age' from the 15th–18th century had reduced the population to a very low level it could well have been overlooked. Thus while it is generally accepted that the cicada in Britain is a relict species the possibility of its being an introduction should not be ruled out.

Fossil cicadas in Britain

The first fossil cicadas were found in Britain nearly 150 years ago but the inadequate descriptions and figures that were published led Handlirsch (1906–08) to consider that they were incorrectly identified. Fossil cicadas are known from the Eocene and Upper Triassic in Britain.

Eocene

The specimen of cicada described from the British Eocene is of considerable palaeogeographic interest and consists of one incomplete hindwing from the Isle of Mull, Scotland (Zeuner 1941: 88; 1944). It was described as *Eotettigarcta scotica* by Zeuner (1944: 110) (Fig. 1), who compared it with Recent *Tettigarcta* (Tettigarctidae) from Australia. While not congeneric, he regarded it as 'very closely related'. (Living Tettigarctidae are restricted to Australia, where the species are associated with an alpine environment, although fossil representatives of the family are much more widespread; Woodward *et al.* 1970). I have re-examined the holotype (In.38883) and have no reason to doubt Zeuner's classification of the fossil on the evidence available. Species of Tettigarctidae have been described from the Triassic and Jurassic of Asia.

Triassic

Several specimens from south-west England were described and figured by Brodie (1845) but only one species, *C. murchisoni*, was named. I have re-examined Brodie's specimens and have additional material from the Upper Triassic.

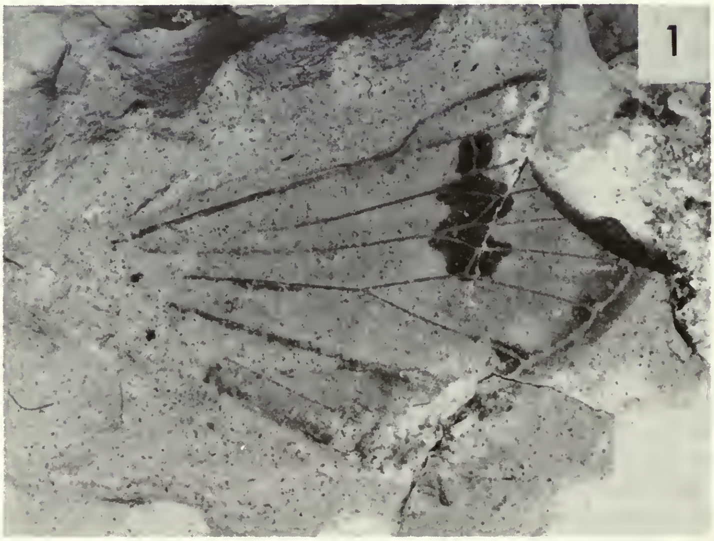
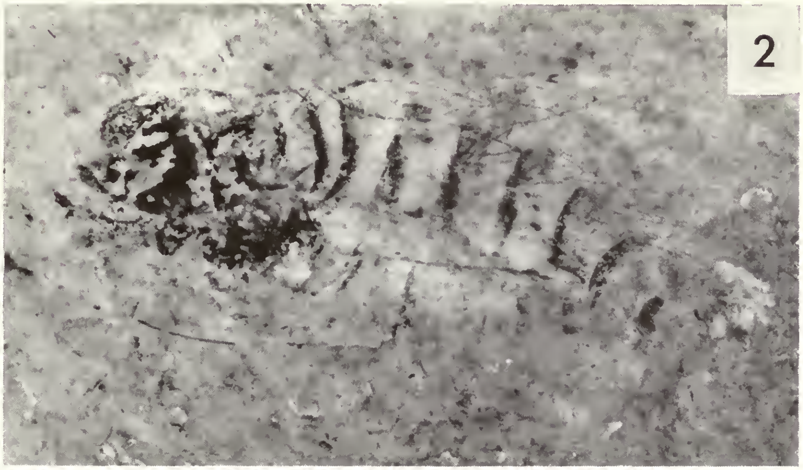


Fig. 1 *Eotettigarcta scotica* Zeuner, holotype. Isle of Mull. In.38883, BM(NH).

The generic classification of Mesozoic cicadas is based entirely on forewing venation (Rohdendorf 1962), making comparison virtually impossible with the incompletely preserved wings of British fossils. All previously described cicadas from the Mesozoic have been placed in the family Tettigarctidae but the character used to separate extant species of this family from the Cicadidae are rarely well-preserved. Woodward *et al.* (1970) separated Recent species of the two families on the presence or absence of tymbals on the dorsal side. However Dr J. P. Duffels (Amsterdam), after examining the specimens, pointed out that the large and separate pro- and mesonotum clearly shown in the British fossils are characteristic of the Cicadidae. The small amount of wing venation preserved also indicates this family rather than the Tettigarctidae. The Cicadidae have not previously been recorded from the Mesozoic.

The most distinctive feature of the British Triassic specimens is the extremely long rostrum. From an examination of Recent cicadas in the British Museum (Natural History) collection it is apparent that the rostrum of the fossils is proportionally longer than the rostrum of most Recent species. However, in the Recent genus *Platypleura* Amyot & Serville there is one species, *P. adouma* Distant (Fig. 4), where the rostrum is much longer than in others of the same genus. Even so, this species does not have a rostrum quite as long as in the fossils. In view of the variation in length of rostrum between species in Recent genera, the description of a new fossil genus based only on this character seems unwarranted.



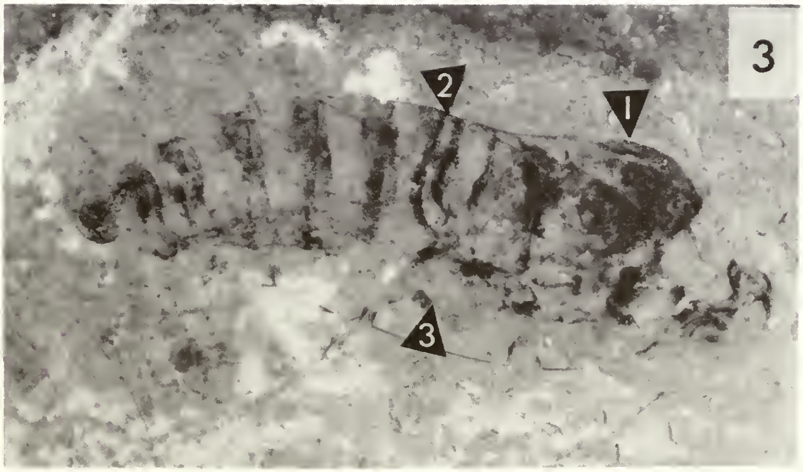


Fig. 2 *Liassocicada ignotatus* Brodie, holotype, ♂. Gloucestershire (Forthampton). In.3539, BM(NH)

Fig. 3 *L. ignotatus*. Worcestershire (Strensham). In.10449, BM(NH). suggested nymphal stage. 1 – possible emergence of imago. 2 – parallel, narrow sclerotized tergites. 3–nymphal wing-pad.

Bode (1953) based the genus *Liassocicada* on the fragment of a forewing from the Upper Lias of Germany, placing it in the Cicadidae. Rohdendorf (1962) more correctly considered it as Cicadoidea *insertae sedis* since none of the characters used to define the family are preserved in the type specimen of *Liassocicada*. However, I propose to redefine this genus and to place the British species in it provisionally.

Systematic description

Family **CICADIDAE** Leach, 1815

Genus ***LIASSOCICADA*** Bode, 1953

TYPE SPECIES. *Liassocicada antecedens* Bode, by monotypy. Jurassic.

Because the definition of this genus is based on a fragment of the forewing it is re-defined here to include *L. ignotatus* Brodie (below).

DIAGNOSIS. Cicadas with elongate rostrum reaching well down the abdomen.

RANGE. Triassic–Jurassic.

Liassocicada ignotatus (Brodie) comb. n.

Figs 2–3, 5–11

1845 *Asilus* (?) *ignotatus* Brodie: 102 [described in the Order Diptera].
1845 *Cicada murchisoni* Brodie: 101; **syn. n.**
1873 Cicada larva, Brodie: 25.
1873 Cicada pupa, Brodie: 25.

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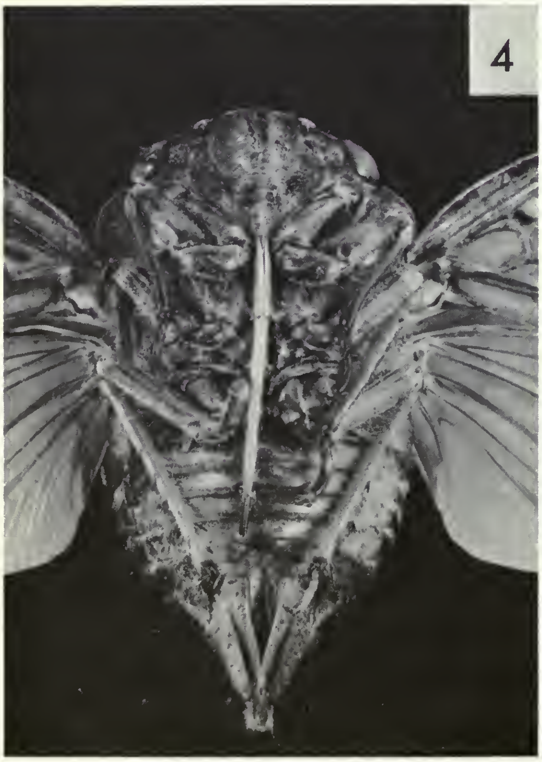

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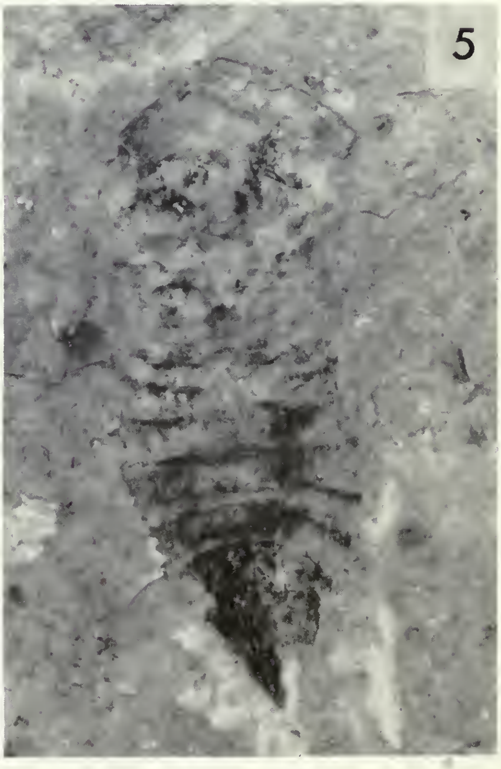


Fig. 4 *Platypleura adouma* Distant, ♀. Recent Africa. BM(NH).
Fig. 5 *L. ignotatus*. Locality unknown. In.59079, BM(NH).

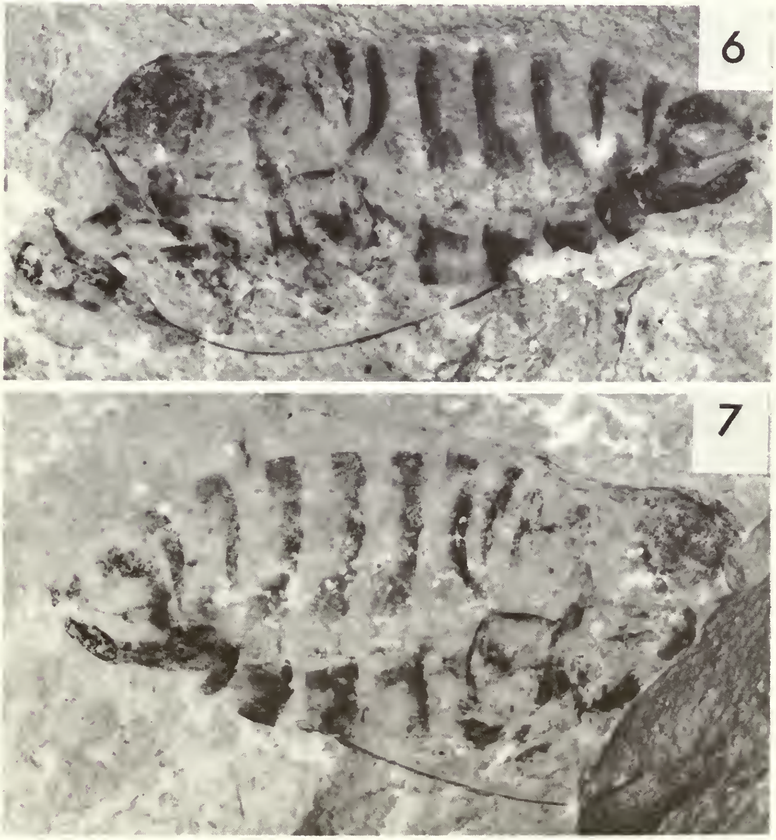
1906 *Asilus* (?) *ignotatus* Brodie; Handlirsch: 503.
1906 *Cicada murchisoni* Brodie; Handlirsch: 504.
1906 Cicada larva, Handlirsch: 511.
1906 Cicada pupa, Handlirsch: 511.

Diagnosis. As genus.

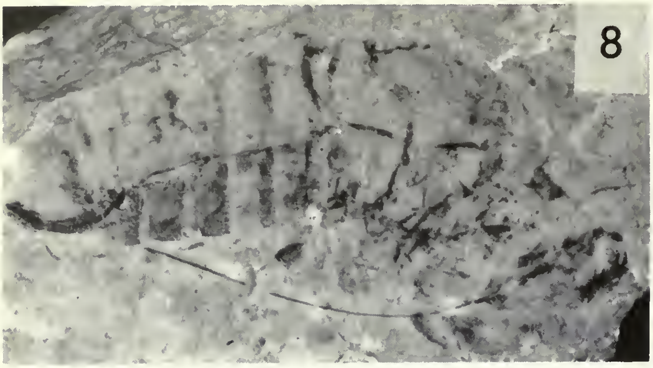
Description. Head with prominent, ridged frons. Eyes large, oval. Rostrum very long, reaching to base of ovipositor in female. Pro- and mesonotum large and separate. Fore tarsal segments rounded, several long spurs on hind tibia. Tympanal organ possibly represented by sclerotization at ventral side of first abdominal segment. Ovipositor short, curved and strongly sclerotized, with sclerotized (?) spermatheca preserved in some specimens (Fig. 10). Specimen In.3539 (Fig. 2) is probably a male, having a rather truncate tip to the abdomen and more slender body than the females. Traces of wing venation are also present on this specimen. Specimen In.10449 (Fig. 3) is probably a nymph, showing the split along the dorsal side of the thorax with (?) partially emerged adult (Fig. 3, arrow 1). [Ocelli, most of wings, tymbal organs not preserved].

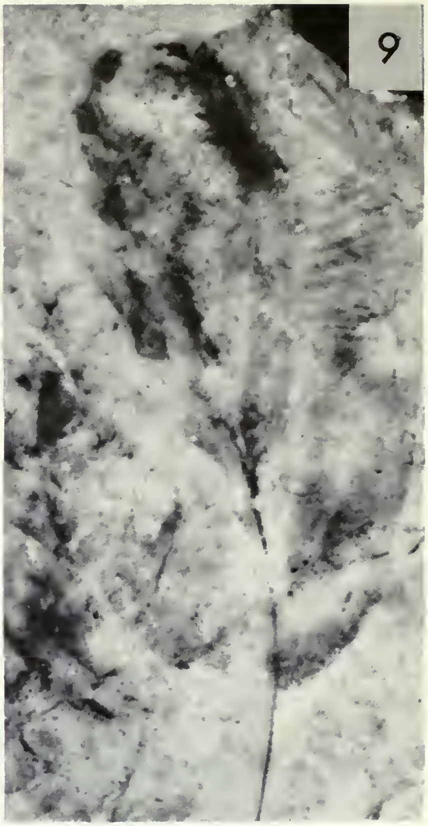
Holotype. In.3539. Forthampton, Gloucestershire; Brodie coll. in British Museum (Natural History). Fig. 2.

Other material. All except the last in British Museum (Natural History) collections.
In.3537. Hasfield, Gloucestershire. Holotype of *C. murchisoni*.
In.10449. Strensham, Worcestershire. Brodie coll. Fig. 3.
In.10440. Strensham, Worcestershire. 'Cicada larva', Brodie coll.



Figs 6, 7 *L. ignotatus*. ♀ [Worcestershire], 'Lower Lias'. IGS GSb 273 (part and counterpart). Institute of Geological Sciences, Geol. Soc. coll. See also Fig. 11.





Figs 8, 9 *L. ignotatus*. Worcestershire (Strensham). In.11244, BM(NH). Fig. 9, head, stylets and ridged frons, enlarged. See also Fig. 10.

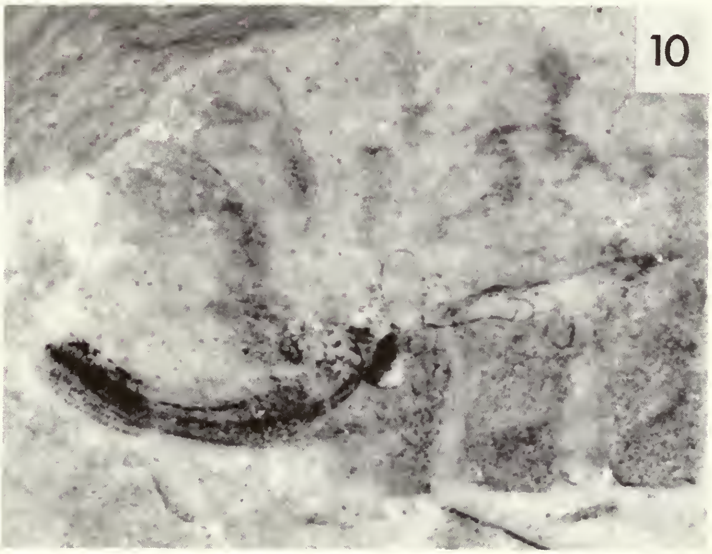
In.11113. Strensham, Worcestershire. Brodie coll.
In.11240. Strensham, Worcestershire. 'Cicada', Brodie coll.
In.11244. Strensham, Worcestershire. 'Cicada pupa', Brodie coll. Figs 8–10.
In.59079. 'Cicada pupa', Brodie coll.; locality unknown but similar in preservation and appearance to the Strensham material. Fig. 5.
IGS GSM GSb 273 [Worcestershire] 'Lower Lias' (no other details); part and counterpart. In Institute of Geological Sciences. Figs 6, 7, 11.

AGE AND DISTRIBUTION. Upper Triassic, Rhaetian Stage; Penarth Group, Lilstock Formation, Cotham Member, *Pseudomonotis* Bed (formerly an 'Insect Limestone'); north-west Gloucestershire and Worcestershire. 'Insect Limestones' have been described by several authors from exposures in Somerset, Avon, Gloucestershire, Worcestershire and Warwickshire, and they are not all at the same horizon. The Insect Limestone in the Tewkesbury and Upton-upon-Severn area from which the cicadas described here were obtained is better called the *Pseudomonotis* Bed, in order to distinguish it from similar beds in other areas which may belong to different horizons. Brodie (1845: 100–102), and more recently Richardson (1948: 143–144; 1966: 153), stated that the bed belonged to the Lower Lias, but most other authorities agree that it was one of the top layers of the 'Rhaetic Beds' (Wright 1878: 14; Richardson 1903: 127–174; 1904: 22, 207–210; Arkell 1933: 107). The confused stratigraphical nomenclature and doubts about its Triassic or Jurassic age have been superseded by the Geological Society's detailed correlations of the British Triassic (Warrington *et al.* 1980) and Jurassic Systems (Cope *et al.* 1981). In the latter report the base of the Jurassic is drawn at the horizon of the first appearance of *Psiloceras planorbis*, and all lower beds (including the lowest part of the 'Liassic Series') belong to the Triassic System. So the *Pseudomonotis* Bed is now firmly established as of Triassic, Rhaetian Stage, age.

Dimensions. Body length 20–25 mm, males smaller than females.

Discussion. Although the name *murchisoni* has page priority over *ignotatus*, and was recognized as hemipterous by Brodie while *ignotatus* was considered dipterous, the holotype of *murchisoni* (In.3537) is not well preserved. Unless the specimen was formerly more complete it is difficult to see why it was considered a cicada. Nothing on it actually rules it out as a cicada but equally only the incompletely preserved forelegs suggest that it might be one: *murchisoni* is here considered a *nomen dubium*. The specimen described as *A. ignotatus* (Fig. 2) by Brodie has the long rostrum characteristic of the other specimens (Figs 3, 6, 7) and is chosen in preference to *murchisoni*.

Dr J. P. Duffels has suggested that In.10449 (Fig. 3) is a nymphal stage, possibly with the emerging adult (arrow 1). There are two parallel sclerites (arrow 2) which are typical of nymphal



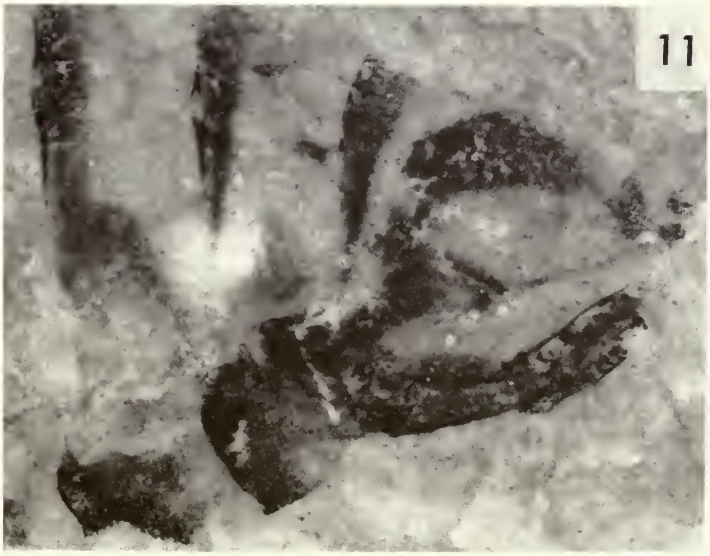


Fig. 10 *L. ignotatus*. Worcestershire (Strensham). In.11244, BM(NH). Ovipositor valves, enlarged. See also Figs 8, 9.

Fig. 11 *L. ignotatus*. ♀ [Worcestershire], 'Lower Lias'. IGS GSb 273, ovipositor valves, enlarged. Institute of Geological Sciences, Geol. Soc. coll. See also Figs 6, 7.

cicadas. The separation of the three thoracic segments is also more clearly shown, suggesting a nymphal instar, and possible wing pads (arrow 3) are indicated. All the other specimens have traces of wings or ovipositors, indicating that they were adults. Cicada nymphs are subterranean with the last instar coming to the surface to moult to the adult stage.

The ovipositor and associated structures are well preserved in most specimens, suggesting a typical strong, slightly curved cicada-type capable of inserting eggs into woody plant tissue. In two specimens (Figs 8, 10) there are associated structures at the base of the ovipositors which may represent the spermatheca but could even have been eggs. Probably the most remarkable structure of the British Mesozoic cicadas is the long rostrum which was at least 14 mm long and in the female reached the base of the ovipositors. The structures actually preserved are the stylets, the elongate maxillae and mandibles with only parts of the surrounding rostrum preserved in a few places. There is no evidence that the stylets were coiled up inside the head capsule, and comparing it with the Recent species (Fig. 4) where the rostrum is also long, it was probably held between the legs. With the humped thorax and typical adpressed head, the method by which the stylets were inserted into the plant tissue is interesting. Aphids with long stylets tend to feed on fissured bark of tree trunks or large roots (Dr V. F. Eastop, personal communication), but it is difficult to see how the Triassic cicadas could insert the long stylets into a plant using the technique of Recent, short-rostrum cicadas. It is possible that its length was important in probing down packed leaf-buds or scales to get at the tissue these were protecting, for example to get at the embryo deep between the scales of a *Pinus*-type cone. It is also possible that the stylets were inserted into plant tissue, but in the absence of evidence from the feeding behaviour of Recent species no further light can be thrown on this remarkable structure.

Acknowledgements

I am indebted to Dr H. Ivimy-Cook, Institute of Geological Sciences, for the loan of some of the specimens and to Dr M. K. Howarth, BM(NH), for advice on the stratigraphy. Dr J. P. Duffels of Amsterdam, Dr W. J. Knight, BM(NH), and Mr E. A. Jarzembowski, BM(NH), examined the specimens and made useful comments, and Dr V. F. Eastop, BM(NH), read the manuscript; to all I offer my thanks.

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The Cephalaspids from the Dittonian section at Cwm Mill, near Abergavenny, Gwent

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Synopsis

An account is given of some fifty articulated specimens of *Cephalaspis* discovered in the mid 1930s by W. N. Croft in a stream section near Abergavenny. All are small animals and are mostly referable to *C. cradleyensis* Stensiö, but three new species *C. cwmmillensis, C. abergavenniensis* and *C.* (*Cwmaspis*) *billcrofti* subgen. et sp. nov. are also represented.

The development and means of distribution of cephalaspids are discussed.

Introduction

An interesting discovery was made by W. N. Croft in the Dittonian (Lower Devonian) of the Anglo-Welsh area some years ago in a stream section in a small tributary of the River Gavenny at Cwm Mill near Mardy, about one mile (1·6 km) north-east of Abergavenny (National Grid ref. SO 311156). Croft in his original field notes records the locality as lying '¾ mile NNE of Asylum, Abergavenny'.[1] Like virtually all the sections and pits in the region that formerly yielded good cephalaspid material the Cwm Mill locality has now been worked out. Here a thin bed of grey-green siltstone, apparently not more than 2 or 3 inches (c. 65 mm) thick, yielded a quantity of articulated specimens of small *Cephalaspis*. Some fifty specimens were collected and doubtless all, or nearly all, must have been complete when first buried, but they were massed together and flattened, lying top-side up, on their backs, even occasionally on their sides, all close together and very often on top of one another. This, combined with the softness of both matrix and specimens, made collecting very difficult and the results were often rather disappointing.

Nevertheless, the collection is of much interest, for articulated specimens from Dittonian strata of the Anglo-Welsh region are extremely rare – Stensiö (1932) recorded only three specimens with part of the body attached – and at undescribed localities only Wayne Herbert, 10½ miles (17 km) away, has produced articulated cephalaspids in a much more diversified fauna (Miles 1973), while a single complete specimen was found in a nodule in a stone-breaker's pile just below Castle Mattock, some seven miles (11·25 km) north of Cwm Mill.

The Cwm Mill section has already been noticed in literature (White 1950: 56; Allen & Tarlo 1963: 145), and although the fauna has never before been described, the cyclothem of which it forms part has been described in some detail and illustrated by Allen (1964: 184–6, fig. 11). Unfortunately, the precise relationship of the Cwm Mill section to the levels of the principal quarries that have yielded the bulk of useful material during the last half century is not known. While those quarries lie in a stable block dipping gently to the south-east and can be related to the 'Psammosteus Limestone' (P.L.), Cwm Mill is in a much less stable area where there is no sign of the P.L., but Allen in his description of the cyclothem states that it 'lies about the middle of the Dittonian stage'.

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[1] The field notebooks of W. N. Croft (1915–1953) are housed in the Department of Palaeontology, British Museum (Natural History).

Bull. Br. Mus. nat. Hist. (Geol.) **37** (3): 149–171 Issued 24 November 1983

It may be convenient at this point to list the principal quarries of the area, with the attendant form of *Pteraspis* (White 1935; 1950: 58 footnote): all are now out of use and largely overgrown:

WERN (or GWYN) GENNI. 650 feet (200 m) above P.L. 6 miles (9·6 km) NW of Wayne Herbert. With *Pteraspis stensioi*.
POOL QUARRY. 350 feet (110 m) above P.L. 3½ miles (5·6 km) SSE of Wayne Herbert. With typical *P. crouchi* and *P. rostrata* var. *waynensis*.
CASTLE MATTOCK (CLODOCK). 240 feet (75 m) above P.L. 3½ miles (5·6 km) south of Wayne Herbert. With *P. jackana* and *P. crouchi* var. *mattockensis*.
WAYNE HERBERT. 220 feet (67 m) above P.L. 11½ miles (18·5 km) NNE of Abergavenny. With *P. rostrata* var. *waynensis*, *P. rostrata* var. *virgoi* and *P. ? jackana* above siltstone lenticle and *P. rostrata* var. *toombsi* in it.
CWM MILL. 'About the middle of the Dittonian stage'. 1¼ miles (2 km) NE of Abergavenny and 10½ miles (17 km) SSW of Wayne Herbert. With *P. ? crouchi*.

The specimens used in the compilation of this paper belong to the collections of the British Museum (Natural History), London and are referred to by register number with or without the prefix P.

The Cwm Mill Fauna

This was a very restricted exposure for the fossil vertebrates; apart from scattered fragments, they occur 'from a distinct horizon' (Allen 1964: 185, fig. 11) over a distance of not more than a foot or two (less than 1 m). Curiously enough Croft in his field notes made very little reference to the discovery of this remarkable assemblage of ostracoderms. Under the heading '*Cwm Mill – Cephalaspis Loc.* (244)' he gives a section 26 inches (0·66 m) in height in which is shown a bed 2–3 inches (c. 65 mm) thick simply labelled 'Pt. (rare) above. Ceph. below': yet from this small exposure an unprecedented number of specimens of *Cephalaspis*, originally complete, were extracted from a single layer, a grey-green siltstone, which seems to have been lenticular.

All the specimens except three seem to belong to a single species, *Cephalaspis cradleyensis* Stensiö, while each of the remainder belongs to a different undescribed species. Outside the siltstone lenticle a darker, harder bed yielded a few fragments of still other species of the genus, in addition to pieces of cephalic discs of *C. cradleyensis*.

The fauna of the siltstone lenticle

Family **CEPHALASPIDAE** Agassiz, 1843

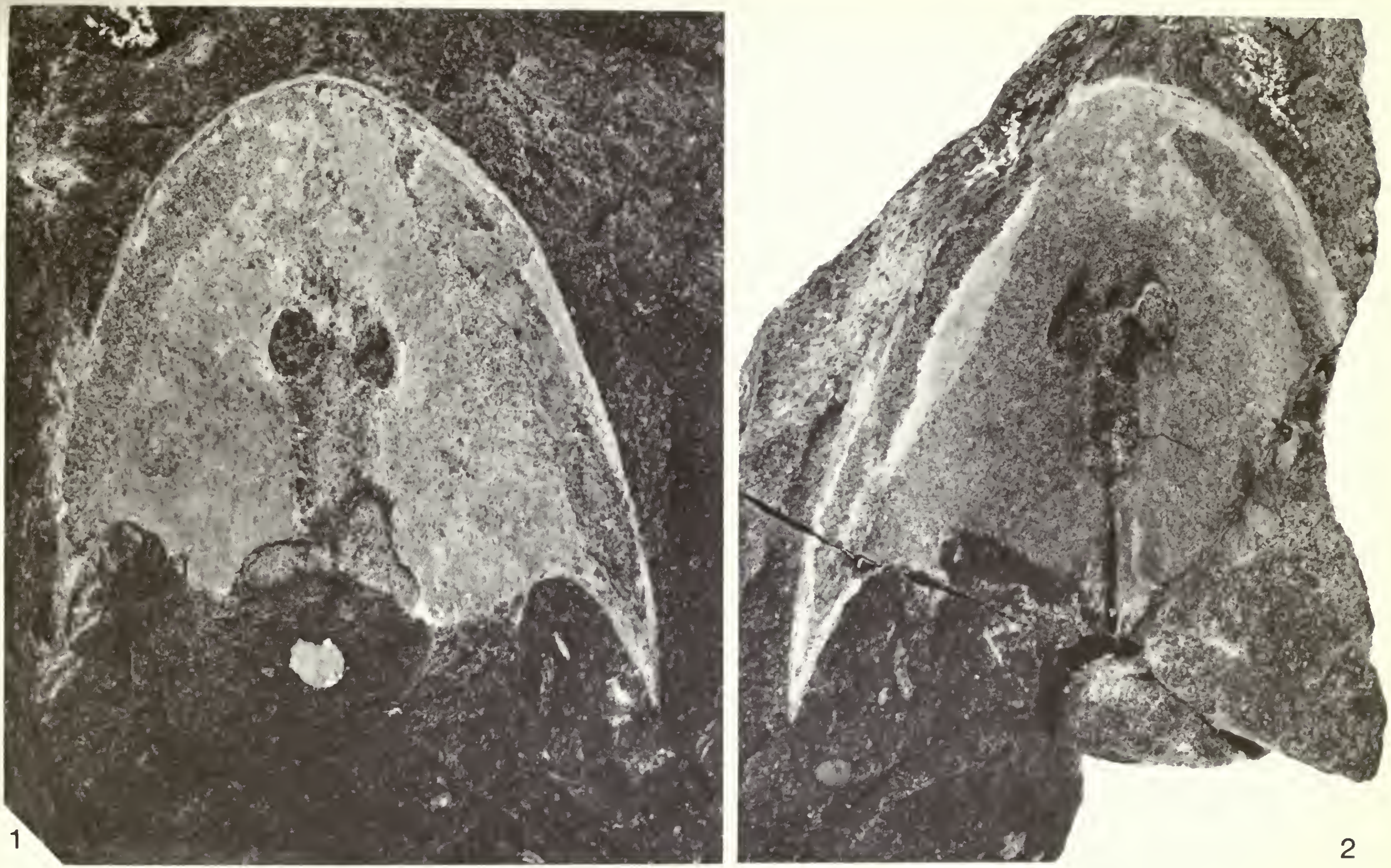
Genus ***CEPHALASPIS*** Agassiz, 1835

Cephalaspis cradleyensis Stensiö

Figs 1–11

1932 *Cephalaspis cradleyensis* Stensiö: 130, text-fig. 44; pl. 15, fig. 6.
1952 *Cephalaspis cradleyensis* Stensiö; Wängsjö: 255, text-fig. 24; pl. 2.

DIAGNOSIS (emended). A small species of *Cephalaspis* with total length 100–120 mm. Cephalic shield about 40 mm long and approximately 40 mm in maximum breadth measured across the tips of the cornua. Lateral margins of shield gently convex, narrowing rather rapidly towards a rounded front without rostral angle. Cornua directed slightly laterally, short, their length scarcely exceeding one quarter of distance between tips and median point of rostral margin; inner margins without denticles. Pectoral sinus rather narrow and shallow; interzonal part broad and short with low but well-defined median crest projecting a little to form a very short posterior angle. Orbital openings somewhat oval and situated rather nearer front than back of shield. Dorsal sensory field long and narrow, about three and half times as long as maximum breadth, and pointed behind. Lateral sensory fields reaching a short distance externally onto surface of



Figs 1–2 *Cephalaspis cradleyensis* Stensiö. Fig. 1, imperfect cephalic shield, the holotype (P.5375), ×2·4. Fig. 2, counterpart of same (P.16960), ×2·4.

cornua. Surface of cephalic shield smooth except for fine denticles around orbits, and with up to twenty rows of fine pits parallel with margins under brim. About 22 rows of scales in front of dorsal fin with at least six ridge-scales.

HOLOTYPE. Cephalic shield P.5375 (Fig. 1); counterpart P.16960 (Fig. 2); Lower Old Red Sandstone, Cradley, Herefordshire.

MATERIAL. Some 42 individuals on 18 blocks, all from Middle Dittonian of Cwm Mill. In some instances a single specimen block contains more than one species and for this reason individuals are separately numbered. The following specimens are from the principal siltstone band: P.22973, P.22974a, b, P.22990–2, P.22993a, b, P.22994, P.22998a, b, P.22999a, b, P.23000a, b, P.23001a, b, P.23002a, b, P.23003a, b, P.23004a, b, P.23005a, b, P.23008–9 (part and counterpart), P.23010a, b, P.23013, P.60867–8 (part and counterpart), P.60869a, b, P.60870–4, P.60875a, b, P.61033a, b, P.61035a, b, P.61036a, b, P.61037–42, P.61043a, b, P.61044a, b, P.61045–6, P.61047a, b. The remainder are from the hard darker bed: P.23006–7 (part and counterpart), P.25100, P.25178–9 (part and counterpart).

Cephalaspis cradleyensis is noteworthy in that it is the only species of the genus so far recorded as being common to the Anglo-Welsh area and Spitsbergen. The original description was based on a single specimen without counterpart from Cradley, Hereford and Worcester, consisting of a small, imperfect and somewhat distorted cephalic shield which certainly did not allow more than a very restricted diagnosis of the species (Fig. 1). This specimen was purchased by the Museum with the H. B. Hill Collection in 1887 but is not recorded by Woodward (1891), possibly on account of its relative insignificance. The counterpart, recorded and figured for the first time here (Fig. 2), was discovered in 1934 in the Museum at Bootle in Lancashire and was then generously presented to the British Museum (Natural History) by the Committee of that Museum. The specimen had been bought originally from the well-known dealer in fossils, J. R. Gregory of London, as an example of *Cephalaspis lyelli*.

DESCRIPTION. Most of the specimens from Cwm Mill are in some respects rather disappointing in spite of their original completeness. The siltstone matrix and the armour of the animals are relatively soft and are often not easy to develop profitably with either tools or acid, and all too often magnification does little to clarify details. All from the siltstone are flattened.

The holotype and its newly figured counterpart have the great advantage of being three-dimensional and show a depth at the back of the skull of 12 mm without the crest and, with the Cwm Mill specimens, it is possible to correct for distortion in regard to the size and form of the cornua, so that a reasonable restoration of the cephalic shield may be made (Fig. 6, p. 155).

The finest of the Cwm Mill slabs (with its counterpart) is undoubtedly that shown in Fig. 3, for on its surface are the remains of at least seven specimens, four of which, labelled in the figure as B (P.22999a), C (P.61043a), D (P.61044a) and E (P.61045), are very nearly complete and show the squamation of the body reasonably well; the fins and tail are, however, poorly preserved. All the specimens except D lie in the usual dorso-ventral position, and as the shields are almost completely flattened the front margins appear entirely rounded, almost semicircular, whereas specimen D lies, most exceptionally, on its side with the cephalic shield almost in lateral profile. A second specimen (P.23003a; Fig. 7, p. 157) is in a similar position.

The total length of a complete specimen with tail would be about 120 mm, with the median length of the head, the body from head to base of tail, and the tail itself all very nearly equal, about 40 mm apiece; and 40 mm is the average maximum breadth, measured across the tips of the cornua, in a flattened cephalic shield. There is one specimen that shows nearly the whole length of the fish, only lacking the tip of its tail (P.23000a, b) and this has approximately the proportions given.

A most typical cephalic shield is P.23008–9 and to this in the counterpart is attached part of the body with the impression of some of the left paddle. The shield is less crushed than many of the other specimens and gives a more accurate impression of the shape. The polygons formed by the inter-areal canals of the mucous canal system are as a rule not visible as the superficial layer of the exoskeleton is continuous, but they do appear occasionally, as in the interzonal part of this

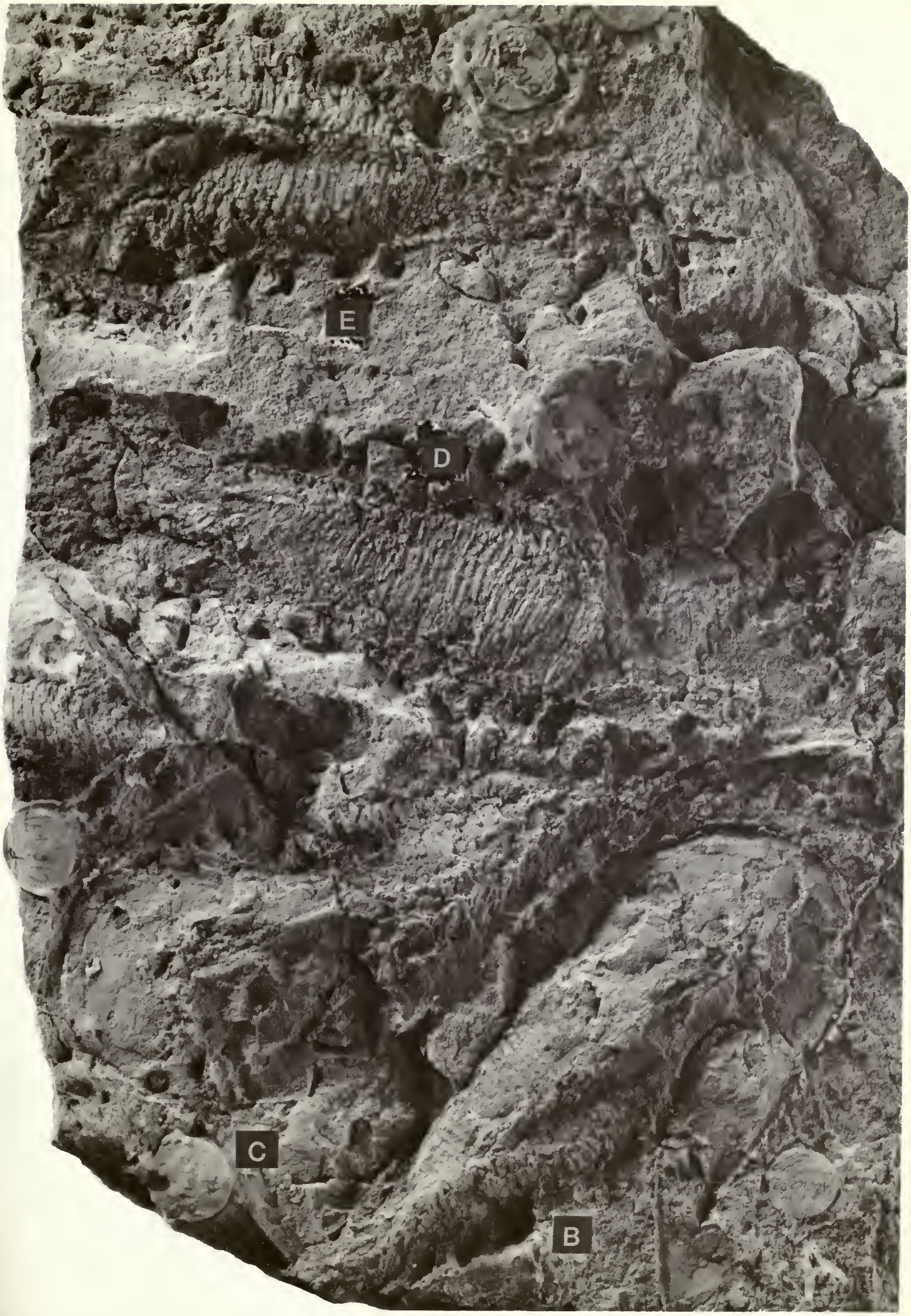
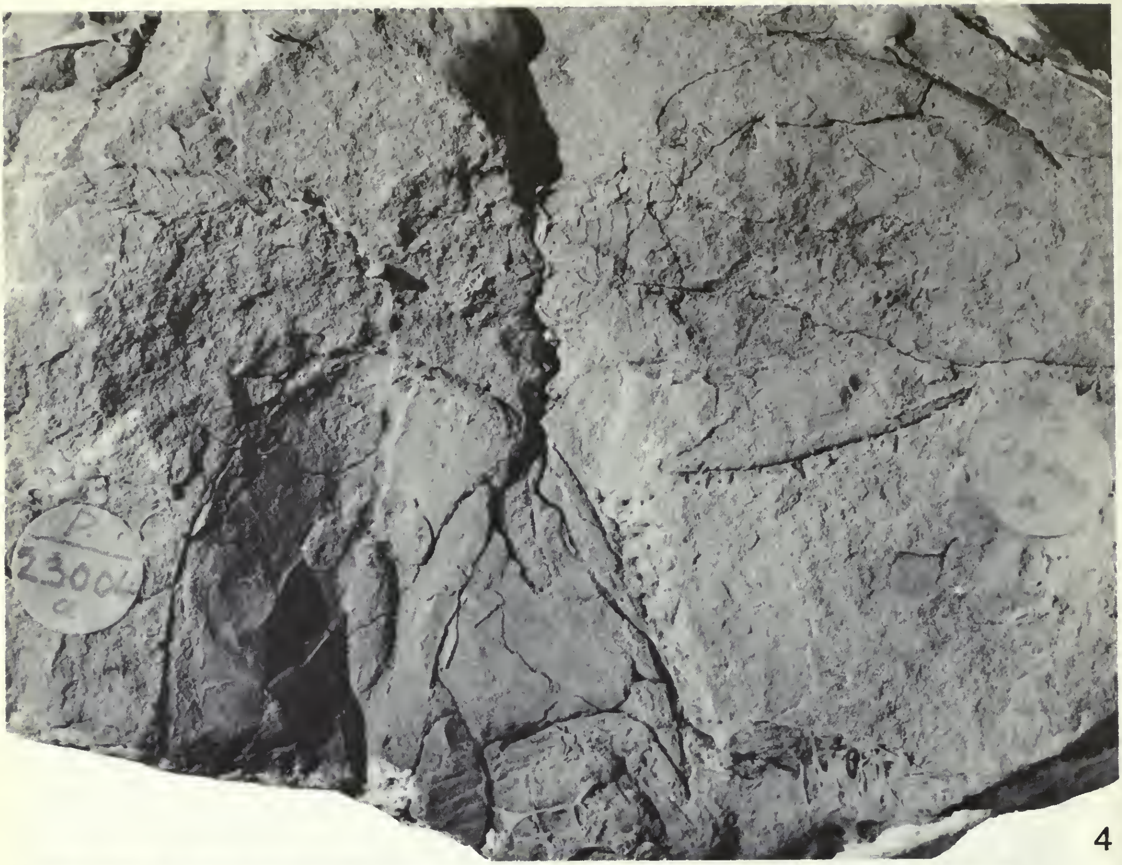


Fig. 3 *Cephalaspis cradleyensis* Stensiö. Siltstone block showing remains of four nearly complete individuals, lettered B (P.22999a), C (P.61043a), D (P.61044a) and E (P.61045). ×1·3.



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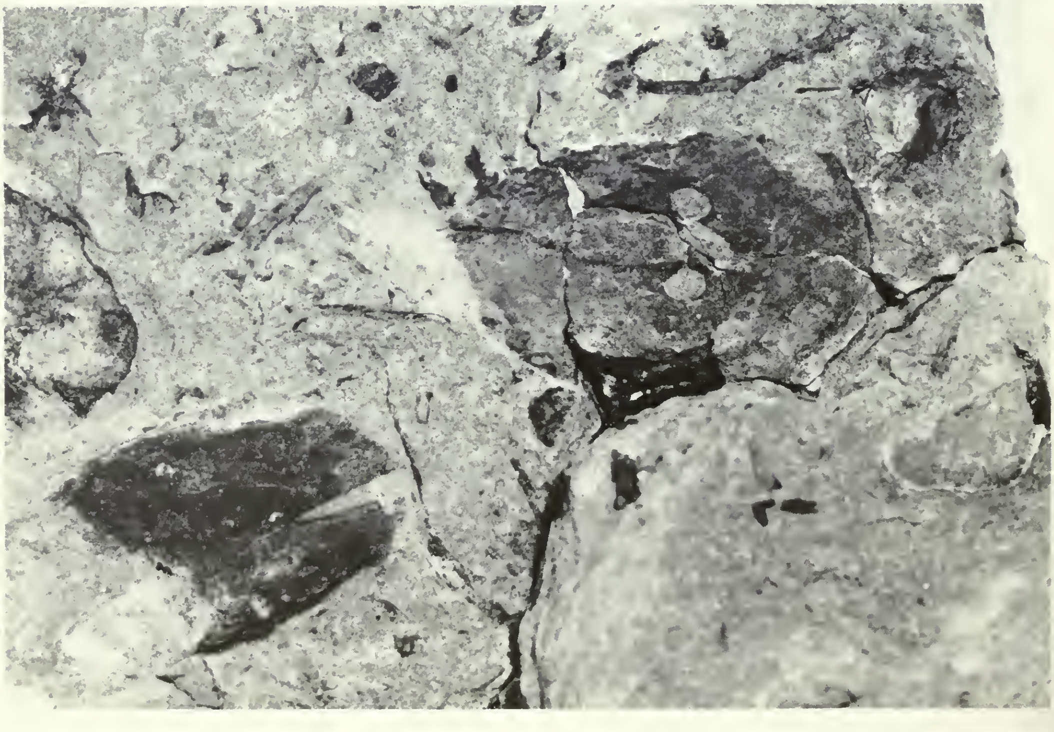

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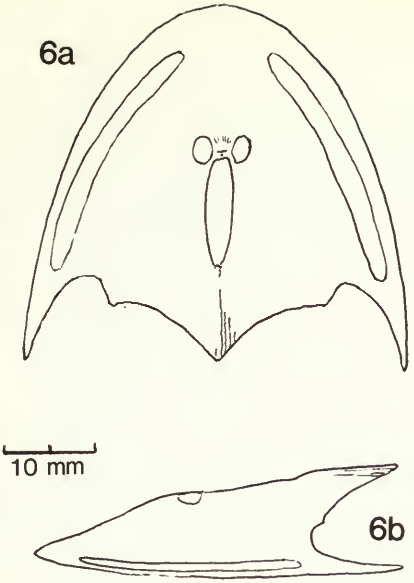

Fig. 6 *Cephalaspis cradleyensis* Stensiö. Restoration of cephalic shield based on holotype (P.5375) and its counterpart (P.16960), and on P.25178–9; in dorsal view (a) and left lateral view (b).

specimen, not naturally but due to the cracking of the convex surface along such lines of weakness under pressure. There is a low but very definite ridge or spine medially on the short but wide interzonal part, with correspondingly narrow and shallow pectoral sinuses.

The best example of the median area of a dorsal shield of *C. cradleyensis* is shown on a piece of the succeeding darker shaly bed (P.25178–9; Fig. 5). The specimen, like the original shield from Cradley, is almost uncrushed, although both sides have been broken away. The median length of the shield is 38 mm; the pineal plate is 16 mm from the rounded anterior margin, while the orbits are each 14 mm away from its centre point. They are oval and measure 4 mm long by 3 mm at their widest. The dorsal sensory field is long and narrow, measuring 12 × 5 mm, and is pointed behind. The lateral sensory fields are 3·5 mm wide in front and are there separated by 6 mm. It is partly on this specimen that the restoration in Fig. 6 is based.

The external surface of the visceral exoskeleton is very well seen in impression in P.60868 (Fig. 10, p. 161): there is the same cover of small scales, numerous and irregular in shape, as Stensiö (1932: 43, fig. 8) illustrated in *Hemicyclaspis*, and there is a similar wide and narrow mouth. In P.23010 (Fig. 9, p. 159), in addition to mouth and scales, there are impressions of at least eight box-like branchial pouches on each side. Curiously enough, each of these two specimens has superimposed on the details of the ventral surface clear impressions of the central features of the dorsal exoskeleton; the orbits, the pineal plate, the circumnasal fossa and part of the dorsal sensory field (Fig. 10)! Branchial pouches, ventral scales and part of the mouth are also to be seen in P. 22993a.

Ornamentation is absent on the upper surface of the cephalic shield except for small areas of minute tubercles around the orbits and the circumnasal fossa. Under the brim of the shield there

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Figs 4–5 *Cephalaspis cradleyensis* Stensiö. Fig. 4, part of a siltstone block: above, in faint outline a whole specimen, probably a juvenile with incompletely developed armour (P.23005a): below, a normally developed cephalic shield (P.23004a); ×1·8. Fig. 5, block from darker rock showing, at top right, an imperfect but well-preserved cephalic shield of *C. cradleyensis* (P.25178); also dorsal and ventral discs of *Pteraspis (Belgicaspis) crouchi* (P.61150), either from a small variety or young specimens, with fragments of plants; ×1·6.

are many rows of minute pittings running parallel with the margin (P.60868; Fig. 10). On the body-scales there are numerous short grooves parallel with the length that vary greatly in definition.

The orbits were said by Stensiö to be 'rather or fairly large', but it must be remembered that the eye-socket is a truncated cone so that the inner aperture in the basal layer, which Stensiö was in fact seeing in the type-specimen, can be, and indeed was, substantially larger than the external opening seen in the counterpart, which was rather on the small side (cf. Figs 1 and 2). They are oval, those in P. 23008–9 measuring approximately 4 mm long and 3 mm wide in a shield measuring 40 mm along the mid-line.

A similar caution should be observed in regard to the length of the lateral sensory fields and the extent to which they are supposed to run onto the bases of the cornua, since their cavity extends beyond the tesselated upper surface; if that is removed the field may appear to go further than it does in fact. In *C. cradleyensis* the lateral sensory fields are narrow and long and do continue on to the short cornua.

The dorsal sensory field is also long and narrow, and in P. 23010b it measures 11 mm in length and 3·5 mm at its widest.

The arrangement of the squamation is much the same as in *C. lyelli* (White 1958*a*), except that the main lateral row appears to be rather deeper and the scales are much subdivided immediately behind the head-shield. The dorsal median scale marking the position of the lost anterior dorsal fin is relatively insignificant. There are approximately 22 scale-rows to the level of the remaining dorsal fin.

The finest tail in the collection is P.22974a, b (Fig. 8, A). It is preserved in a completely lateral position. Unfortunately all the cephalic shield is lost so that the specific identity of the specimen is not absolutely sure, but although the body is a shade larger than in other specimens, it does show similar features. The cut-water scales of the dorsal fin are large and six or seven of them are very well seen, and there are at least 32 ridge-scales along the upper margin of the tail-fin. Between the latter and the main squamation of the tail and again between the main squamation and the ventral fin-rays there are single rows of minute longitudinal scales. There are more than fifty main rows of scales on the tail. The 'fin-rays' are formed of very small scales in rows that bifurcate at least twice to form the fringe of the tail-fin.

Remains of the 'horizontal antero-ventral lobes of the tail' (Heintz 1939: 112) or 'ventral axis of caudal fin' (*vhp.* in Stensiö 1932: pl. 34) may be seen in this and other specimens but nowhere to advantage.

The pectoral fins or paddles are represented in several specimens, usually by impressions of the basal part, but in P.23002a there is a faint but complete impression of the left fin (Fig. 7, top). It is 13 mm in length with a maximum breadth of 6 mm. The shape is rather leaflike with a gently convex outer margin and a slightly sinuous inner margin, forming a rather broad terminal point. The scales on the limb are as usual largest at the base, diminishing in size distally and marginally. This specimen is of the usual size, with the cephalic shield 40 mm in median length.

The specimens in the darker bed (P.23006–7, P.25100 and P.25178–9) are all imperfect isolated cephalic shields, associated with broken dorsal and ventral discs of *Pteraspis* cf. *crouchi*. As noted before, in spite of their imperfections, the specimens from this bed are much better preserved in detail and less crushed than the more complete specimens from the main bed.

Uncrushed shields of *Cephalaspis cradleyensis* are very simple in form and at a glance not unlike small editions of the genotype, *C. lyelli*, but even so there are no species recorded from the Anglo-Welsh or Spitsbergen areas with which this species may be confused except that represented by the unique specimen from the latter province which Wängsjö (1952: 255, fig. 24; pl. 2) placed in *C. cradleyensis* itself. However, there do seem to be differences between that specimen and those from the Anglo-Welsh area. The latter do not show a rostral angle nor denticles along the inner margins of the cornua (Figs 1–2), as Stensiö averred in his original description of the species (1932: 130, fig. 44; pl.15, fig. 6). These features do not appear to be very obvious in either of the figures in Wängsjö's plate. It is probably safer then to label the rather poorly preserved, unique specimen from Spitsbergen simply as '*Cephalaspis* cf. *cradleyensis*' and to await further discoveries.

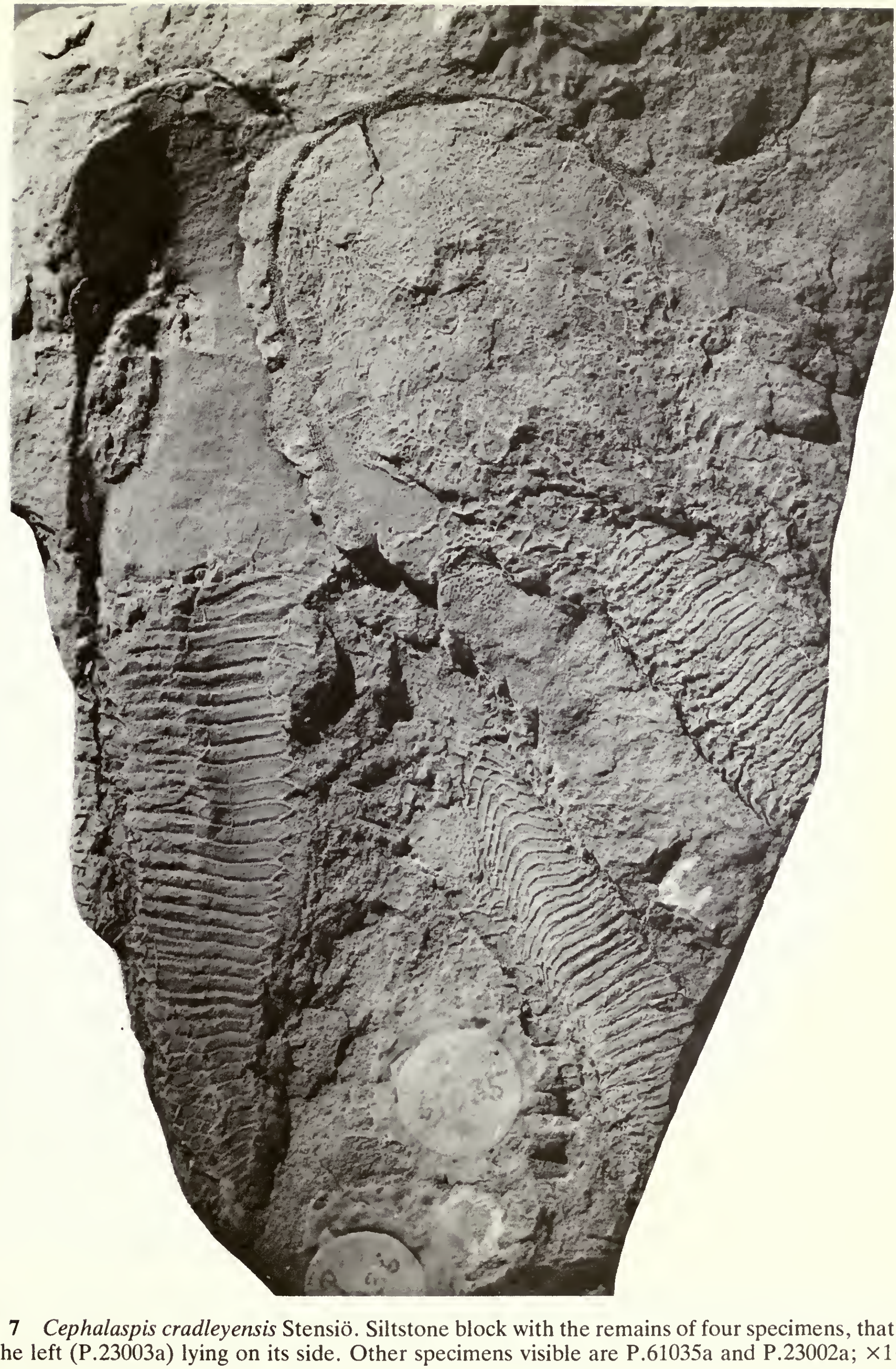

Fig. 7 *Cephalaspis cradleyensis* Stensiö. Siltstone block with the remains of four specimens, that on the left (P.23003a) lying on its side. Other specimens visible are P.61035a and P.23002a; ×1·9.

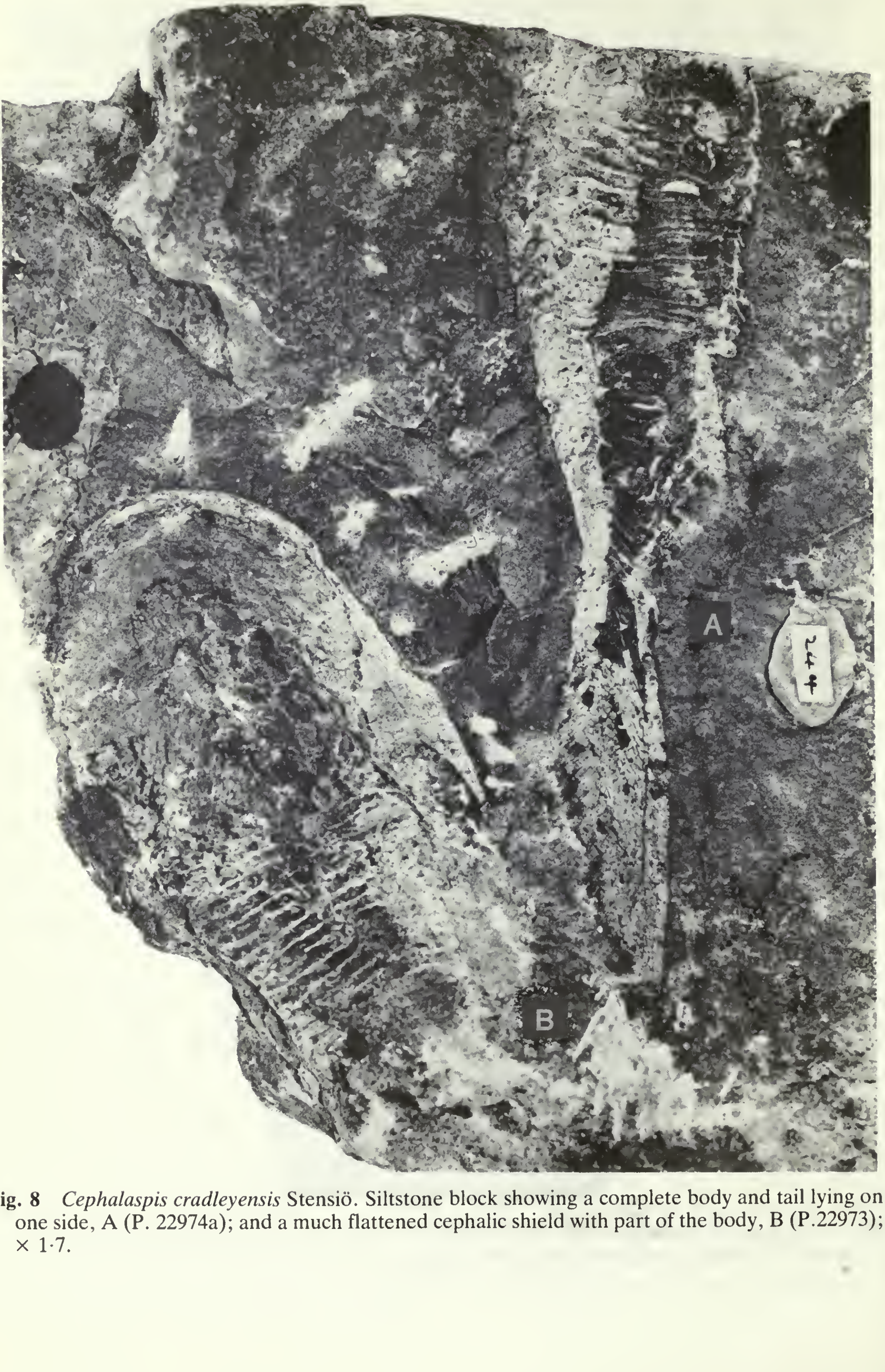

Fig. 8 *Cephalaspis cradleyensis* Stensiö. Siltstone block showing a complete body and tail lying on one side, A (P. 22974a); and a much flattened cephalic shield with part of the body, B (P.22973); × 1·7.

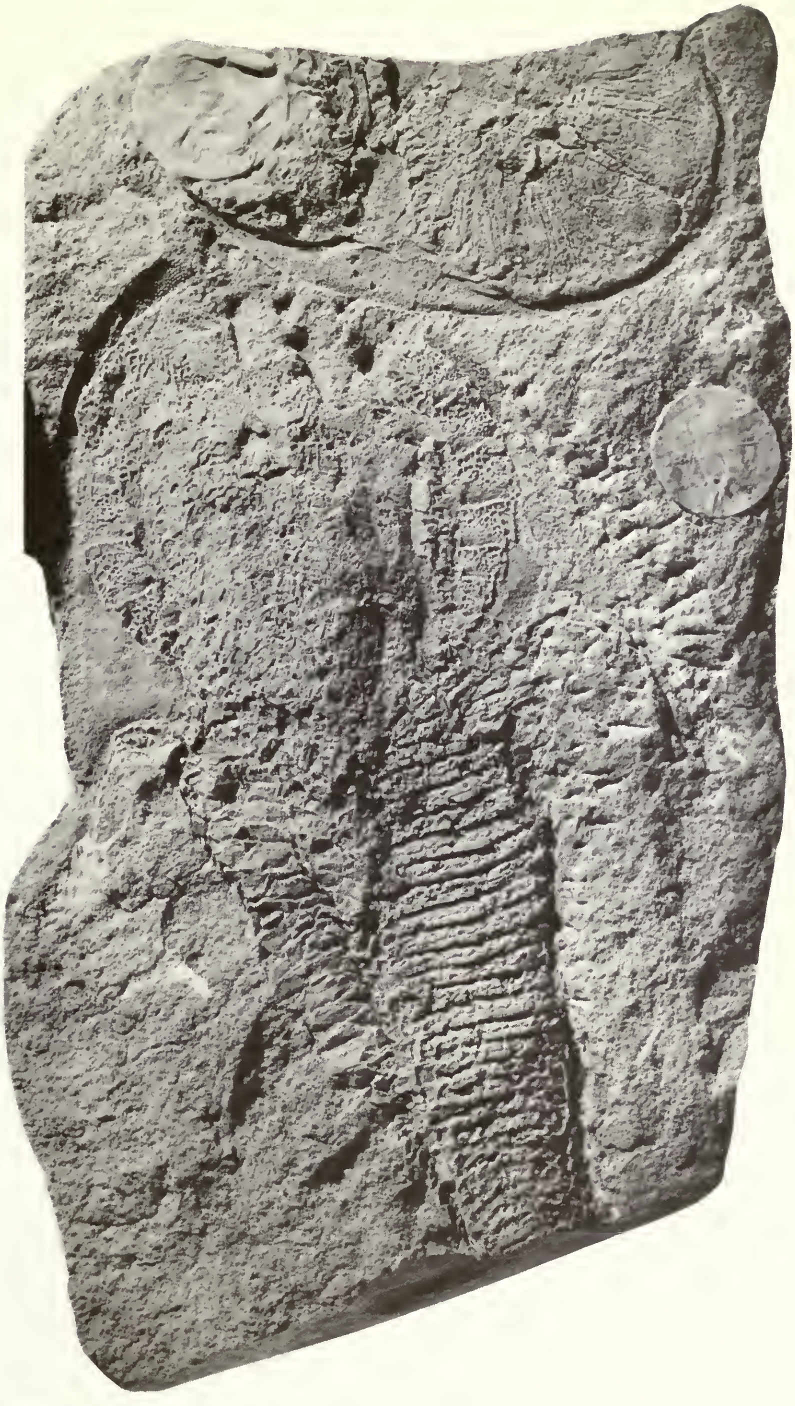

Fig. 9 Siltstone block with two specimens of *Cephalaspis*. The larger specimen (P.23010a) is an example of *C. cradleyensis* and shows the impression of most of the lower surface of the body and almost all the undersurface of the cephalic shield with mouth, scales and branchial pouches on each side. The smaller specimen at the top (P.23011a) is the **holotype** of *C. cwmmillensis* sp. nov. which shows the inner impression of the head and the ventral impression of the right cornu. ×2·1.

Cephalaspis cwmmillensis sp. nov.
Figs 9, 12–14

Diagnosis. A species of *Cephalaspis* of very small size with maximum breadth of cephalic shield, at base of cornua, about 1·25 times as great as length of shield in median line. Shield narrows evenly in front without rostral angle and with sides forming a continuous curve with cornua. Cornua broad at base but narrowing rapidly to a fine point distally and curving gently inwards to a level a little behind that of posterior interzonal angle. The distance from the cornual tips to the centre of rostral margin about 3⅓ times as long as the length of the cornua. Inner margins of cornua without denticles. Pectoral sinuses narrow and deep. Interzonal part short and broad, its breadth between posterolateral angles being about half maximum breadth of shield, with low median ridge. Posterior angle of interzonal part approximately a right angle, reaching well behind posterolateral angles. Dorsal sensory field narrow, nearly four times as long as broad and blunt behind. Lateral sensory fields narrow and short, not reaching onto cornua. Orbital openings relatively large, oval in shape, lying considerably nearer pectoral sinuses than rostral margin of shield. Small independent pineal plate present. Exoskeleton ornamented with numerous minute thorn-like denticles.

Holotype. Imperfect cephalic shield in counterpart P.23011a, b: Middle Dittonian, Cwm Mill, Abergavenny, Gwent. The only specimen.

Description. This shield is reasonably well preserved, its deficiencies being largely due to difficulties in collecting. Originally doubtless much of the body was attached, but as it is, the left cornual region and the whole of the body has been lost save for the impressions of a few fragments of body-scales and of the base of the right paddle on the counterpart. The right cornu lay under the cephalic rim of a head shield of a specimen of *C. cradleyensis* described above (Fig. 9). The specimen of *C. cwmmillensis* is one of the few specimens from this locality that show fair impressions of any of the vessels of the head (Fig. 12).

The median length of the shield is approximately 28 mm and the estimated maximum breadth, across the base of the cornua, is 34 mm. The breadth of the interzonal part between the posterolateral angles was about 16 mm; the length of the surviving cornu is 10 mm and the distance of its tip from the centre of the front margin of the shield is 34 mm; the distance of the pineal foramen from the posterior tip of the shield is 14 mm and about the same from the rostral end, so that the oval orbits were approximately at the middle of the length of the shield but very much nearer to the pectoral sinuses than to the rostral margin. They measure 3 × 2·25 mm.

The shield is not especially broad but a notable feature is the almost even, continuous curve of the sides and cornu, and although the anterior margin does narrow rather quickly, there is certainly no rostral angle and the inner margin of the broad-based but sharply pointed cornu is smooth. There is some evidence that the interzonal part bore a low median ridge.

The dorsal sensory field is moderately long but almost evenly narrow, and truncated at the posterior end. It measures $2{\cdot}5 \times 8$ mm and is about 7 mm from the posterior point of the interzonal aprt. The lateral sensory fields are also narrow and appear to have been unusually short, stopping some little distance from the base of the cornua.

The exoskeleton is represented by the impression of the external surface only, and this shows that the upper surface was covered with very small thorn-like denticles, while under the brim there were numerous rows of interrupted fine ridges parallel with the outer margin of the shield. The mucous canal system was apparently entirely enclosed in the exoskeleton.

The internal cast shows the impressions of a number of features rarely seen in this fauna, such

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Fig. 10 Impression of cephalic shield of *C. cradleyensis* Stensiö showing decoration of the submarginal rim and the ventral scales of the anterior half; and also impressions of the eyes, the circumnasal fossa, the pineal plate and the anterior end of the median sensory field (P.60868). ×3·1.

Fig. 11 Part of siltstone slab with **holotype** of *Cephalaspis abergavenniensis* sp. nov. (P.61034b). ×2·1.

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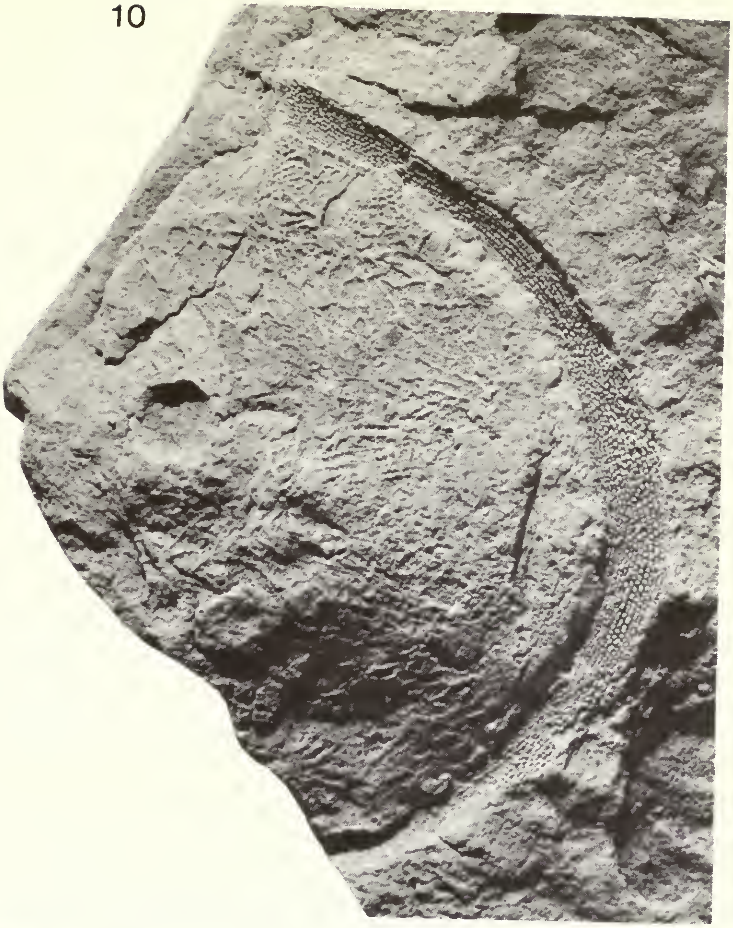

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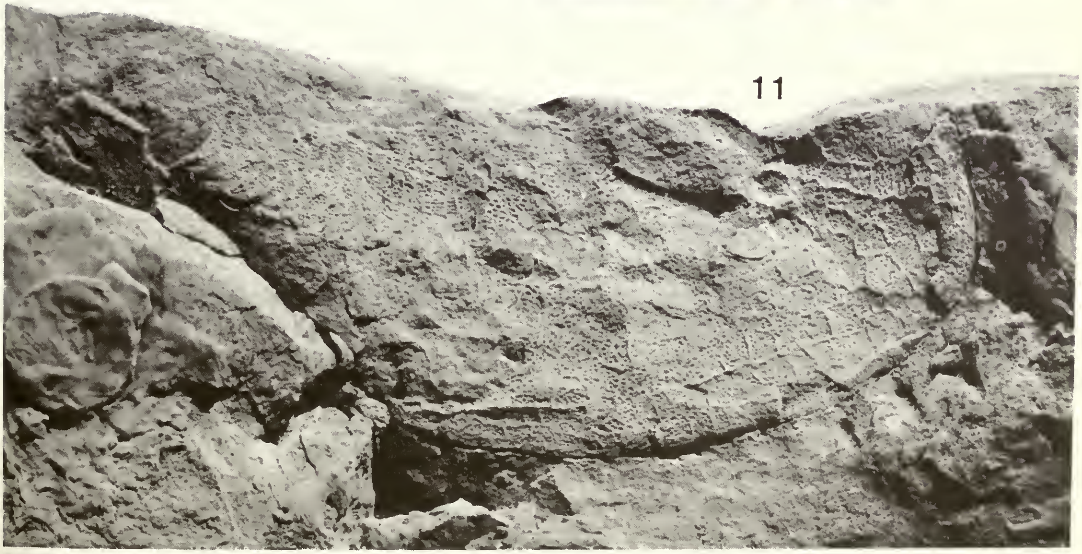
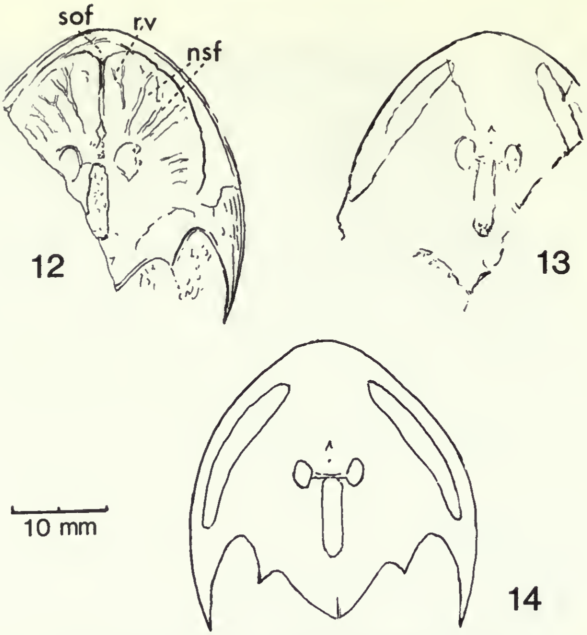




Figs 12–14 *Cephalaspis cwmmillensis* sp. nov. Fig. 12. Dorsal view of holotype (P. 23011a). The anterior part has been destroyed and shows impressions of a number of internal features: **nsf,** canals of nerves of lateral sensory field; **rv,** rostral vein; **sof,** supra-oral field. Fig. 13. Counterpart of holotype (P.23011b) showing impression of external surface. Fig. 14. Outline restoration of cephalic shield.

as the supra-oral field, the aortic groove, the naso-hypophysial openings, canals of nerves of the lateral sensory fields, and of a rostral vein.

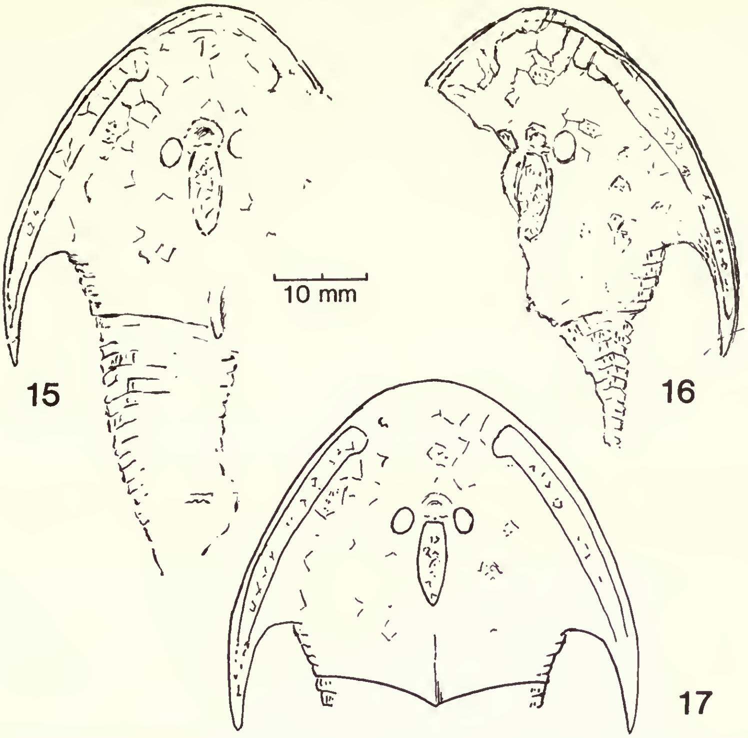
REMARKS. The only other species of *Cephalaspis* from the Anglo-Welsh area similar to *C. cwmmillensis* is *C. heightingtonensis* Stensiö (1932: 97; pl. 14, figs 5–7), but that species is even smaller and relatively broader, and among other obvious differences, the orbits are further forward, the cornua have denticles along the inner margins, and the pectoral sinuses are shallower.

Among the several species comprising small individuals from Spitsbergen described by Wängsjö (1952) none bears much resemblance to *C. cwmmillensis*, and the same remark applies to those from Scotland described by Stensiö in 1932.

Cephalaspis abergavenniensis sp. nov.

Figs 11, 15–17

DIAGNOSIS. A small species of *Cephalaspis* with maximum breadth of headshield, at tips of cornua, about 1·25 times as great as length of shield in median line. Shield narrows rapidly and evenly forward without forming rostral angle but with sides in continuous curve with cornua, which are rather stout and of medium length, pointing almost directly backwards and reaching somewhat beyond level of interzonal median angle; inner side without denticles. Pectoral sinuses rather narrow and very deep. Interzonal part broad and long with very obtuse median posterior angle and clearly comprising at least five rows of body-scales, with low median crest projecting only slightly behind. Dorsal sensory field elongated oval in shape, three times as long as maximum breadth. Lateral sensory fields extending well onto cornua. Orbital openings situated well in front of middle of median length, about equidistant from centre of rostral margin and pectoral sinuses. Small independent pineal plate present. Circumnasal fossa large with



Figs 15–17 *Cephalaspis abergavenniensis* sp. nov. Fig. 15. Dorsal view of holotype (P.61034a). Fig. 16. External impression of counterpart of holotype (P.61034a). Fig. 17. Restoration of holotype.

prominent rim. Outer parts of exoskeleton of shield conspicuously subdivided into polygonal areas by circum-areal mucous grooves. Ornament of exoskeleton of shield of numerous small but well separated stellate tubercles, increasing slightly in size and becoming thorn-like towards back of shield and ridge-like on scales of body.

HOLOTYPE. An imperfect cephalic shield with much of the body attached, in counterpart, P.61034a, b: Middle Dittonian, Cwm Mill, Abergavenny, Gwent. The only specimen.

DESCRIPTION. This small specimen is reasonably well preserved and was certainly complete when first collected, but now lacks the caudal half of the body and part of one side of the head-shield, and even more of the body in the counterpart. It lies on a slab with the remains of at least three specimens of *C. cradleyensis*.

The median length of the cephalic shield is 36 mm and the maximum breadth, flattened, is 44 mm across the middle of the cornua; the breadth of the interzonal part between the posterolateral angles was about 24 mm. The length of the cornu is 12 mm, and the distance of its tip from the centre of the rostral margin is about 44 mm. The distance of the pineal plate from the posterior angle of the shield is 20 mm and from the rostral margin 15 mm, so that the orbital openings are much nearer to the front of the shield: they are about 14 mm from the pectoral sinuses and are oval, measuring 3 × 2·5 mm.

A small independent pineal plate is present and the circumnasal fossa is large with a conspicuous rim.

The shield is rather broad at the level of the cornua, but it narrows fairly quickly towards the front without forming a rostral angle.

The interzonal part is 24 mm broad between the posterior lateral angles and is long, being clearly made up of five or six body-scales which are incompletely fused at the sides. There is a short, low median ridge well separated from the median sensory field in front of it, which scarcely protrudes beyond the very obtuse posterior angle.

The median sensory field is elongate-oval in shape, measuring approximately 9 × 4 mm, and the lateral sensory fields are long and narrow, well separated in front, where there is a small expansion, and behind they pass for some distance onto the cornua.

The surface of the shield is divided into moderately-sized polygons by the mucous grooves which, as usual, are much smaller on the sensory fields.

The surface of the shield is ornamented with small but conspicuous stellate tubercles, which become somewhat larger and more thorn-like backwards towards the body and become short ridges on the squamation. There are impressions of parts of about 20 rows of scales to be seen.

REMARKS. Like the other diminutive single-specimen species associated with *C. cradleyensis* at Cwm Mill *C. abergavenniensis* is readily distinguished from any other species recorded from the Anglo-Welsh areas or from Spitsbergen, in this instance by its simple, rather wide cephalic shield, the 'craquelure' of the outer surface, the long interzonal part with its marked composite scale-structure and short, low median ridge, together with its very diminutive size.

Subgenus *CWMASPIS* nov.

DIAGNOSIS. Small species of *Cephalaspis* with very wide cephalic shield, almost semicircular, without rostral angle but with very short cornua not even reaching level of acute posterior angle of very brief and broad interzonal part with low, small median ridge. Pectoral sinuses very shallow with no denticles on inner side of cornua. Dorsal sensory field long and narrow, oval, pointed at rear; lateral sensory fields not extending onto cornua and widely separated in front. Orbital openings situated well in front of middle of median length of shield and considerably nearer to rostral margin than to pectoral sinuses.

TYPE SPECIES. *Cephalaspis billcrofti* sp. nov. (only species).

REMARKS. The great breadth and shortness of the whole shield and the interzonal part with the extreme brevity of the cornua readily distinguish this species from all others and give it a likeness superficially to some forms of *Benneviaspis*, but the shape of the sensory fields and the position of the orbits are those of a true species of *Cephalaspis*.

Cephalaspis (Cwmaspis) billcrofti sp. nov.
Figs 18–20

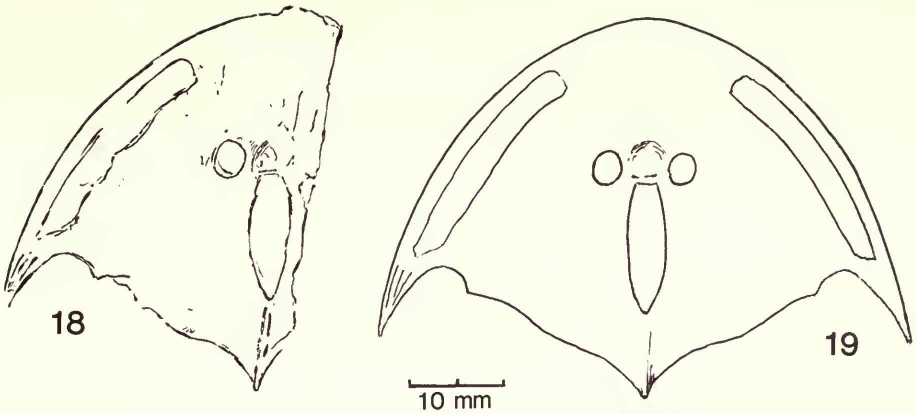
DIAGNOSIS. As for subgenus (only species).

HOLOTYPE. Imperfect head shield P.23012, Middle Dittonian, Cwm Mill, Abergavenny, Gwent. The only specimen.

DESCRIPTION. This small cephalic shield has lost nearly all the right side but there is sufficient remaining for the whole to be reconstructed (Fig. 19).

The shield is extremely wide and short and the surviving cornu is very short indeed, probably not exceeding 10 mm in length, without any denticles along the inner edge. The front margin of the shield forms a continuous curve from side to side with no suggestion of a rostral angle and the maximum breadth, across the tips of the cornua, was approximately 56 mm, and the median length only some 40 mm: even so, the point of the median posterior angle was some 7 mm behind the level of the tips of the cornua. The interzonal part of the shield was very short but broad, measuring about 40 mm between the posterolateral angles which lie far forward, so that the pectoral sinuses were very shallow and narrow, and the posterior border is somewhat sigmoidal between the posterolateral angles and the slightly projecting median point formed by a short and shallow median ridge.

The dorsal sensory field is 13 mm long, in shape an elongated oval, pointed behind, with a maximum breadth of about 4 mm. The lateral sensory field preserved is short and pointed



Figs 18–19 *Cephalspis (Cwmaspis) billcrofti* subgen. et sp. nov. Fig. 18. Dorsal view of holotype (P.23012). Fig. 19. Restoration of holotype.

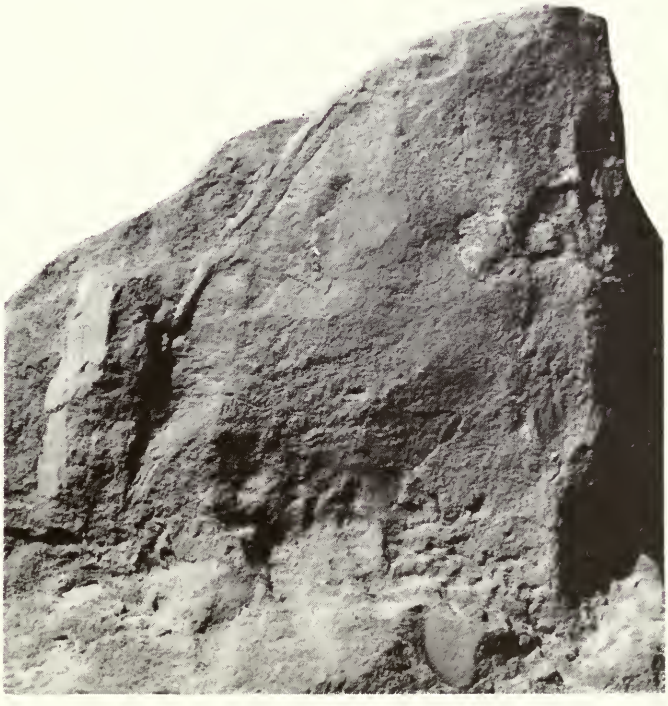


Fig. 20 *Cephalaspis (Cwmaspis) billcrofti* subgen. et sp. nov. Dorsal view of **holotype** (P.23012); ×2·1.

behind; it does not reach onto the cornu. Anteriorly the lateral sensory fields must have been widely separated.

The orbital openings were situated well in front of the middle of the median length of the shield and measure approximately 4 × 3·5 mm.

A separate pineal plate is present, lying some 15 mm from the centre of the anterior margin and about 22 mm from the tip of the posterior angle of the interzonal part. The circumnasal fossa is conspicuous.

The exoskeleton has a fine granular surface.

REMARKS. There is no other species of *Cephalaspis* with which this form may be confused. It is named for W. N. (Bill) Croft who discovered this interesting section in the course of a comprehensive study of the Lower Old Red Sandstone of the area which unhappily he did not live to complete.

Summary of the fauna of the siltstone lenticle:
Cephalaspis cradleyensis Stensiö – About 40 specimens
Cephalaspis cwmmillensis sp. nov. – One specimen
Cephalaspis abergavenniensis sp. nov. – One specimen
C. (Cwmaspis) billcrofti subgen. et sp. nov. – One specimen.

The fauna of the 'Darker Bed'

The so-called 'Darker Bed', of which the siltstone lenticle presumably forms part, is to be found in Units 2 or 3 of the cyclothem at Abergavenny described by Allen (1964: 184–7, fig. 11). The fauna is not only different from that of the lenticle but very differently preserved: instead of being crowded together, flattened and comprising complete animals, the fossils are well separated, three-dimensinal and broken usually into fairly large pieces, and bodies (with one exception) and tails are completely absent. *Cephalaspis cradleyensis* is present but rare in the material collected (Fig. 2), but dorsal and ventral discs of young or a small form of *Pteraspis (Belgicaspis) crouchi* are common, as are plant fragments. There are also three substantial pieces of a much larger species of *Cephalaspis* than *C. cradleyensis*, and of these two may well be parts of the same cephalic shield (P.22995–7). One specimen shows a round orbital opening about 5 mm in diameter and lanceolate dorsal sensory field 14 mm long with a maximum breadth of 3·5 mm; the other specimen has a low but distinct dorsal crest on the interzonal part; in both the outer surface is smooth.

The third piece has a short but powerful cornu 22 mm long directed slightly outwards, a rather narrow pectoral sinus and part of a narrow lateral sensory field running onto the cornu.

There is yet another specimen from the 'Darker Bed' that is worth a mention for, although very imperfect, it is clearly different from any of the other specimens recorded from the locality and part of the body is preserved in impression. The matrix is different; although dark it has red rustlike markings and is very sandy, so that the specimen (P.60872) is extremely fragile. It shows the impression in counterpart of the ventral surface of the left cornu and the left side of the body as far as the base of the tail, and there is a faint outline of perhaps three-quarters of the cephalic shield. The total length of the animal preserved was approximately 65 mm, while the maximum breadth of the shield at the level of the tip of the cornu is estimated at 44 mm. The cornu itself at 15 mm is relatively long and there is no sign of denticles along the inner margin. It is 4 mm broad at its base. The pectoral sinus is deep and rather narrow. The outlines of the small ventral scales are in places well shown with fine horizontal ridges. There are just enough characters to make it clear that it does not belong to the same species as any of the other specimens of *Cephalaspis* from Cwm Mill but insufficient to carry identification further. Much the same may be said of the three larger fragments from the 'Darker Bed' already described, and they cannot be positively associated with any of the congeners from the type-locality of *C. cradleyensis* (Stensiö 1932: 200).

The occurrence of specimens of *Cephalaspis*

The wide range in time and space of the cephalaspids (Wängsjö 1952: 9–14; Halstead & Turner 1973: 74, figs 7–9), in particular of the type genus *Cephalaspis* Agassiz (*sensu lato*), at one time promised to provide a valuable means of correlating and dating the strata of the Lower Old Red Sandstone in its several apparently discrete areas. But as Wängsjö rather sadly remarks in his admirable monograph on the cephalaspids of Spitsbergen (1952: 585), 'for a safe correlation with other areas . . . the Spitsbergen Cephalaspids are in general of fairly little importance . . . as the species apparently were not very widespread'. Only two forms, *C. cradleyensis*, then a very rare species form the Anglo-Welsh Borders, and a new variety of the Scottish *C. powriei*, each represented in Spitsbergen by a single very imperfect cephalic shield, provide tenuous links with other areas. Further, we may note that no species as yet has been recorded as common to the neighbouring Scottish and Anglo-Welsh areas.

Worthwhile specimens of *Cephalaspis* are not so very common considering the very large regions and the thickness of Lower Devonian non-marine strata from which specimens have been collected for many years. The Spitsbergen material, on which Stensiö (1927: v–ix) based his classic anatomical studies, dates from collections made from 1909 to 1926, but these specimens and those collected in 1939 on which Wängsjö based his researches (1952) were much less satisfactory from the purely systematic point of view, and thus for precise correlation, owing to natural imperfection of the specimens and so to the relative scarcity of those that could be clearly named specifically. Wängsjö could identify satisfactorily only about 160 specimens of the genus from the combined Red Bay and Wood Bay formations, while more than 20 species were based on single imperfect cephalic shields. As Wängsjö himself remarked (1952: 249), 'In such cases the diagnosis is, of course, only preliminary', a comment that is unhappily of almost universal application.

The specimens from the Midland Valley of Scotland are very different in their state of preservation, especially in Angus (Tayside) in the north-eastern part, where numerous nearly complete animals have been found (Stensiö 1932: pls 25, 28, 30–40, 43, 46). In some quarries they are flattened, but in others the shape of head and body has been well maintained, as with the lectotype of *Cephalaspis lyelli* Agassiz (White 1958*a*), and isolated cephalic shields also occur uncrushed.

The specimens of *Cephalaspis* so far descibed from the Anglo-Welsh Borders resemble those of Spitsbergen in consisting almost entirely of isolated cephalic shields: indeed, out of a total of about 65 specimens recorded by Stensiö (1932) only three had part of the body attached. Although on the whole much better preserved in regard to external features they show very little indeed of the internal anatomy.

The first specimens of *Cephalaspis* were described by Agassiz (1835), yet after nearly a century Stensiö (1932), in his comprehensive monograph of the cephalaspids of Great Britain, could muster no more than 141 worthwhile specimens for the record, 77 from Scotland and 64 from England. Doubtless other specimens were unaccounted for, simply because they were unknown or not available to the author at the time the monograph was written, but even so the numbers are strikingly small. In the Anglo-Welsh area the relative scarcity of specimens is in great measure due to the high degree of cultivation of the land and its generally flat topography. Moreover, the Lower Old Red Sandstone there is in general too soft to occasion large-scale quarrying for building material. Indeed, until fairly recent times much of the collecting seems to have been done rather casually by amateurs, largely from the labourers in small temporary pits opened up for farming or other local purposes. This does perhaps explain the all too frequently poor condition of the specimens and also the very common separation or loss of valuable counterparts, with the consequent loss of important information in the description of rare species: one may note that of the twenty-three species and varieties of the genus *Cephalaspis* described from Great Britain by Stensiö fifteen type specimens have no known counterparts to date. Four have counterparts shared by different institutions, and of the other four species now with counterparts three had the two sides, or parts thereof, reunited after many years of separation. The lectotype of *C. lyelli* Agassiz was reunited after 36 years (20087, presented by Sir Charles Lyell in 1846; P.3233, in the Enniskillen collection 1882); the holotype of *C. lankesteri* after 58 years (45943 in the Lightbody bequest 1874; P.16155 originally in the Hereford Museum and presented to the BM(NH) in 1932); and the holotype of *C. cradleyensis* after 47 years (P.5375, H. B. Hill collection 1887; P. 16960, Bootle Museum presentation 1934 – as related above, p. 152). The only instance of a holotype and its counterpart being kept together in all the Scottish and Anglo-Welsh material described by Stensiö is that of the little cephalic shield of *C. heightingtonensis* which was purchased complete in 1864.

The growth and distribution of *Cephalaspis*

Questions relating to the individual growth, original source and dispersal of the Agnatha in general have long been matters of discussion. As regards the cephalaspids and the genus *Cephalaspis* in particular, it has long been noticed that no juvenile stages have ever been recorded, and Westoll (1945, 1946, 1958: 192), Denison (1947, 1951, 1956) and White (1958*b*) on this and other grounds came to the not unreasonable conclusion that 'at least many cephalaspids acquired their bony skeleton only when fully grown'. That this was so seems now to be generally accepted (Wängsjö 1952: 247). Such a late development of the armour fits in very well, as an adult character, with the idea that the earlier Osteostraci were entirely soft-bodied, which in turn does away with a major objection to the theory that the Agnatha were marine or at least coastal in origin by explaining the absence of their remains in salt-water deposits. Such an environment would readily explain their very wide and relatively swift distribution. Even so, it is still rather difficult to explain the complete absence of partly grown specimens, rapid though the development of hard parts may have been. Clearly it is a matter of habitat and where such a metamorphosis could have taken place – obviously not in the area of formation of the usual Lower Old Red facies. There is in fact just one specimen in the collection from Cwm Mill that seems to show incompletely formed hard parts. This specimen (P.23005a, b; Fig. 4, p. 154) is slightly smaller than average specimens of *C. cradleyensis* and is worth special consideration. It is a whole animal with tail and is on the same surface of rock as a normally-developed example of *C. cradleyensis*. Like that specimen, it is completely flat and in counterpart, yet only the outlines of its various features can be seen: it is just a ghost of a specimen. It cannot have been dissolved away after entombment, for nothing has affected the adjacent specimen, which is perfectly normal in its condition: it does suggest very strongly a young animal in the early stages of forming its armour. If this interpretation of the fossil is correct it indicates that ossification took place evenly more or less throughout the animal.

From the acquisition of the hard parts at full growth stage and the subsequent inability to expand further, it follows that all specimens of a species should be roughly of the same size. Therefore size was a specific character, and this seems to have been tacitly understood in the composition of specific diagnoses. Wängsjö (1952: 247), in writing on the Spitsbergen forms, remarks that 'the shields preserved are always from full grown individuals . . . the variation on the length of the shield in a single species seems to be at most about 20% of the mean length.' However, the range in size of some of the British species as described by Stensiö (1932) seems to have been much greater than was anticipated: that is, if the identifications are accepted as correct.

The following are the variations in the median length of the cephalic shield in five forms, with percentage variation:

C. salweyi	80 to 145 mm in 14 specimens	80% variation.
C. whitei	45 to 70 mm in 21 specimens	65% variation.
C. pagei	20 to 60 mm in 32 specimens	200% variation.
C. powriei brevicornis	51 to 78 mm in 8 specimens	53% variation.
C. powriei asper	60 to 80 mm in 6 specimens	33% variation.

The first three species certainly call for further consideration and answers may lie between preservation and identification: certainly more than one species is covered by *C. whitei* as originally described.

Other general questions relating to the species of the genus concern the actual habitat and the proliferation of species at the same level and locality.

The later Dittonian deposits, in which the remains have been found most abundantly in the Anglo-Welsh region, have been admirably documented and discussed (e.g. Allen & Tarlo 1963: 398, Allen 1964: 194, Allen 1979): we may note that 'the Dittonian facies of the Welsh Borderland has been interpreted as the deposit of a floodplain complex' and comparison made with the modern sediments of the Colorado Delta and River (Allen 1963: 398). The climate was 'probably warm to hot' (Allen 1974: 152), at any rate in the not so distant Clee area, and that according to authors there quoted southern Britain was on 'the borders of a major arid zone' or 'in the southern hemisphere within a few degrees of latitude of the Devonian palaeomagnetic equator'.

However, there are one or two important points that invite further comment. Allen & Tarlo (1963: 144–6) state that 'During early Dittonian times . . . the vertebrates must all have been freshwater living' and 'in the main have been transported downstream after death', and again in the Ditton Group that 'Although the vertebrates show evidence of water sorting and transportation after death, and some were clearly reworked through the floodplain, there can be no doubt that as in the "*Psammosteus*" Limestones Group, the animals inhabited the fresh waters of rivers.' Lastly, Allen (1979: 67) remarks that in his distal alluvial facies 'The vertebrates emerge as channel-dwellers for at least part of their lives, their remains tending to accumulate, after much reworking, in the lag deposits formed on the channel floors.'

It is undoubtedly true that the cephalaspids were inhabitants of fresh waters, not of the rivers in the floodplains to which their distintegrated remains were commonly carried by stream action, but as inhabitants of the upper reaches, the head waters, lakes and the like, from which sometimes the complete animals were swept by storm action, generally dead and decaying but occasionally still alive and subsequently dying when the resultant pools dried up. The floodplains and the annectent rivers and channels were not the natural environment of the cephalaspids, they were their mortuaries and graveyards. The statement (Allen & Tarlo 1963: 146) that 'The majority of the cephalaspids were obviously able to survive considerably longer [than the pteraspids and a few cephalaspids] in such an unfavourable environment' as had existed at the time of the Cwm Mill or of any other deposition must be considered a misinterpretation of the facts.

The species of *Cephalaspis* were evidently poor swimmers. Their forelimbs were not primarily paddles to aid in progression but balancers to check the depressing effect of the relatively large and somewhat incongruous heterocercal tail, virtually the only means of propulsion, and of the heavy armoured head.[2] Active animals would not require so complete a protection as in these creatures, and the flattened undersides of both head and body as well as the form of the transverse mouth clearly proclaim them as bottom-living scavengers largely suctorial in their feeding; as such they would not fare very well in the intermittent torrents and rivers of the floodplains. The idea of carriage from a considerable distance is clearly supported by the rarity of the preservation of the body or its elements, so manifest in the Spitsbergen and Anglo-Welsh provinces.

Comment has already been made on the way in which cephalaspids, along with other Agnatha, 'generally appear at particular horizons only, and are replaced by entirely different forms' (Allen & Tarlo 1963: 151). This indeed may be so, but the evidence so far published in regard to the systematics of the cephalaspids and to the relative levels of the known localities leaves much to be desired, especially in the two provinces in Great Britain. The further remark that 'This individuality can best be explained by postulating a series of immigrations to the Anglo-Welsh Province, . . . as the presence of some of the genera and species in such distant Provinces as Podolia and Spitzbergen can only be accounted for by a faunal interchange via the sea' conjures up the interesting but unlikely picture of endless waves of naked young cephalaspids, constantly differing in species, largely local in origin but with an occasional intruder from foreign parts, assembling in estuaries from time to time over millions of years, waiting to don their armour prior to facing the dangers of fluviatile ascent. Further, the notion that these seemingly sluggish bottom-feeders should have in any way anticipated the life-wanderings of either salmon or eel seems an even nearer approach to the realms of fantasy.

---

[2] The suggestion of Janvier (1978: 22) that 'ces nageoires étaient capables de mouvements latéro-mésiaux importants' on the evidence of supposedly special smooth areas on the dorsal and ventral surfaces of the cornua 'chez presque tout les Céphalaspididés' is certainly not acceptable as a general rule, at least for the earlier, more typical species of the genus *Cephalaspis* (s.l.), for of the twenty species recorded from Great Britain by Stensiö (1932) no less than eleven bear spines or denticles along the inner margins of their cornua, and of these eight are described as having also narrow pectoral sinuses, a combination that would have made the movement of fins up and down past the level of the cornua impossible without damage. From the Red Bay Series of Spitsbergen out of thirty-seven recorded species nine had the double handicap of denticles and narrow sinuses, but in the succeeding Wood Bay Series in only one species are such denticles said to have been present. That species had a very wide head-shield with very wide pectoral sinuses, like most of the other species known from the formation, a trend that certainly would have allowed freedom of movement to the pectoral fins.

Wängsjö (1952: 570–1) gives a good generalized idea of the coming-in and disappearance of cephalaspids and doubtless provides a pattern for the occurrence of the genus *Cephalaspis* in other provinces, that is, of the intermittent appearance of apparently unrelated species, often several at a time but differing in number and very restricted in time and usually in area, but generically covering a very great period of time and thickness of strata. The injection of fresh species at irregular intervals is not acceptable if it is agreed that the cephalaspids were originally soft-bodied and marine in habitat and only developed hard parts when fully grown and established in fresh water. An endless succession of such metamorphoses taking place over the millions of years that the genus spanned seems less than likely, nor is the development of almost endless congeneric species in the open sea a probability.

If, on the other hand, *Cephalaspis* was first established in fresh waters, it was likely to have been much more active in its original unarmoured condition that in its ultimate adult development, allowing the animals to ascend the rivers to the quieter permanent headwaters in the 'distant land masses' in the north of 'Euramerica' (Young 1981: 226, fig. 1). These waters were possibly in the form of large connected lakes or inland seas, rather after the pattern of those in central Africa (White 1950: 58), and may have been sufficiently extensive to cover the drainage systems of all the Cephalaspid Province. At this stage adult armour was presumably developed against newly-encountered earlier resident predators, such as eurypterids and large acanthodians (Miles 1973), and subsequent diversificaton must have taken place in these relatively quiet waters after the manner of the living cichlid fishes in Africa (Greenwood 1974). It is interesting to note that Greenwood (1974: 112) records that in Lake Victoria 'over 150 species [of the genus *Haplochromis*] have evolved within little more than three-quarters of a million years, from one or at most a few closely related species', and that in the smaller Lake Nabugabo five endemic species of the same genus have evolved since the lake 'was isolated from Lake Victoria by a sand spit formed some 3500 years B.P.' The analogy cannot, of course, be taken too far, since one is dealing with different animals, and at vastly different periods of time, and there is one major factor in the speciation of the cichlids that the cephalaspids lack, and that is variation in dentition and hence in diet. Heintz (1940: 181–2) has indeed indicated some differences in the external details of the oral area in some cephalaspids but there is no indication of change in their microphagous diet.

If the major habitat of the cephalaspids was, as has been suggested, in the fresh waters of the distant uplands, it would explain the spasmodic appearance of their remains in the floodplain deposits, as the results of overflow following unusual rainfall in the region of the headwaters. The generally disarticulated condition of the fossils resulting, with very rare exceptions, in nothing but isolated cephalic shields, was due to the distance corpses were carried and the time that it took, and the readiness with which the flimsy, lightly attached scales would be dispersed and carried away once decay had set in.

That very occasionally there should occur very local, usually lenticular deposits in which complete animals with the bodies and fins intact are to be found, as at Cwm Mill and Wayne Herbert, is to be expected as a result of the floodwaters from exceptionally violent storms in the uplands rapidly carrying still living or moribund animals down the rivers to be immediately entombed in the drying-up pools of the warm floodplains. That the lenticle in the somewhat younger section at Wayne Herbert should have yielded a much more widely diversified fauna than at Cwm Mill is merely a reflection of the local circumstances at the time.

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The relationships of the palaeoniscid fishes, a review based on new specimens of *Mimia* and *Moythomasia* from the Upper Devonian of Western Australia

By B. G. Gardiner

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The relationships of the palaeoniscid fishes, a review based on new specimens of *Mimia* and *Moythomasia* from the Upper Devonian of Western Australia

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Synopsis

Two species of palaeoniscids are described from the Frasnian of Gogo, Western Australia: *Mimia toombsi* Gardiner & Bartram, and *Moythomasia durgaringa* Gardiner & Bartram. A detailed account of their head structure, appendicular and axial skeletons and squamation is given in a series of accounts of regional anatomy. Each account is accompanied by a discussion of the salient features in which comparison is made with living and fossil actinopterygians as well as all other major gnathostome groups. In the course of these comparisons previously-described material of *Cheirolepis, Acanthodes*, various placoderms, hybodont sharks and cephalaspids is reinterpreted.

The Western Australian genera are similar in many respects, including the pattern of the dermal bones of the skull, cheek and pectoral girdle. *Moythomasia* has a short, blunt snout with small premaxillae separated by a toothed rostral, and a palatoquadrate with a short anterior ramus. *Mimia* has a longer, hooked snout with large premaxillae which meet in the mid-line, excluding the rostral from the jaw margin, and a palatoquadrate with a long anterior ramus. *Moythomasia* shows one marked advance over *Mimia* in the possession of a rudimentary ascending process on the parasphenoid.

The most striking primitive features of the Gogo palaeoniscids are the incomplete cranial fissure in which the ventral otic fissure was cartilage-filled and separate from the perichondrally-lined otico-occipital fissure, the presence of a lateral cranial canal, dermohyal, basal and fringing fulcra, a perforated propterygium, and the assumed enclosure of the adductor mandibulae muscle by the palatoquadrate and dermal cheek bones.

The principal anatomical conclusions concern the history of the myodome and trigeminofacial chamber, and the spiracular canal.

The ossification patterns of the skull roof, cheek, palate, lower jaw and shoulder girdle of osteichthyans are reviewed critically. It is concluded that there are two distinct dermal roofing bone patterns and that an operculogular series is a primitive gnathostome attribute whereas submandibulars are a sarcopterygian synapomorphy.

The principal conclusion about the interrelationships of actinopterygians is that the Palaeonisciformes are a paraphyletic group. *Mimia* and *Moythomasia* are stem-group actinopterans whereas *Cheirolepis* is a basal actinopterygian. Most other palaeoniscids are stem-group neopterygians and may be inserted between the Chondrostei and the Neopterygii.

The principal broader phylogenetic conclusions concern the interrelationships of the sarcopterygians and the relationships of the chondrichthyans and placoderms. The Porolepiformes are considered to be the sister-group of the choanates, the placoderms the sister-group of the osteichthyans and the chondrichthyans the primitive sister-group of other gnathostomes.

Introduction

The first aim of this paper is to make known the palaeonisciform fishes from the Devonian Gogo Formation of Western Australia.

The specimens were mainly collected in 1967 by a joint expedition from the British Museum (Natural History), the Western Australian Museum and the Hunterian Museum, Glasgow (Brunton, Miles & Rolfe 1969; with references) at Gogo Station, a cattle property some 250 km SE of Derby in the Fitzroy Trough. The Fitzroy Trough lies on the northern flank of the Canning Basin, with its northern limit faulted against the Kimberley Plateau, a stable Precambrian block (Playford & Lowry 1966). The Canning Basin was apparently land during the Middle Devonian, with a southern shore-line near its junction with the Kimberley Plateau. In the late Devonian the Canning Basin slowly subsided, leaving much of the Fitzroy Trough as a near-shore shelf (the Lennard Shelf) some 300 km in length and several km wide. Both fringing and atoll stromatoporoid and algal reefs grew upon this shelf, with typical reef development including reef, back-reef, fore-reef and inter-reef facies. The Gogo Formation is inter-reef and composed of shales and siltstones with thin bands of limestone and numerous calcareous concretions. About half of the calcareous siltstone concretions contain fossils, chiefly phyllocarid crustaceans and fishes (Gardiner & Miles 1975). The formation is well dated on palaeontological grounds as Frasnian 1α– to 1β (Roberts *et al.* 1972; with references). Since Devonian times weathering has removed much of the softer inter-reef deposits of the Fitzroy Trough, leaving the fossil-bearing concretions lying on the surface. A map of the Gogo Formation localities is given by Miles (1971*b*: fig. 1). A few specimens were collected on an earlier expedition by H. A. Toombs of the British Museum (Natural History) in 1963.

The fishes have been prepared by the standard acetic acid techniques and one specimen (*Mimia*) has been serially sectioned. The specimens are uncrushed and often almost complete, which suggests that the concretions themselves developed during an early stage of diagenesis in still-water conditions.

The second aim of this paper is to discuss certain aspects of actinopterygian comparative morphology that may have a bearing on the problems of actinopterygian relationships and interrelationships. Thus the anatomical descriptions are divided into several parts each of which is followed by a discussion section. The discussions are intended to establish or propose primitive conditions in various groups (i.e. synapomorphies of those groups). Wherever possible homologies are established by congruence with other characters, but in some cases the criterion of commonality is used. I have also employed ontogenetic precedence and outgroup comparison as well as the stratigraphical succession in helping to establish the polarity of transformation series.

The term 'palaeoniscid' is used throughout for those fossil fishes which have traditionally been included within the extinct Palaeonisciformes. 'Actinopterygian' is used for any member of the group Actinopterygii, 'actinopteran' for members of the Actinopteri (Rosen *et al.* 1981) and 'osteichthyan' for bony fishes plus tetrapods. 'Sarcopterygian' refers to members of the Actinistia plus Choanata, while the term 'rhipidistian' is used for Osteolepiformes, Porolepiformes and Youngolepididae.

Specimen numbers are prefixed as follows: BMNH, British Museum (Natural History); RSM, Royal Scottish Museum; GSM, Institute of Geological Sciences, London.

Lettering used in text figures

aasc	anterior ampullary chamber
acv	foramen of anterior cerebral vein
aesc	external ampullary chamber
af	area of fusion between occipital arch and otic capsule
a.ghy	area of attachment of geniohyoideus muscle
ahy	groove for afferent hyoidean artery
aip 1	articular facet for first infrapharyngobranchial
alig	area of origin of aortic ligament
amyd	dorsal anterior myodome
amyv	ventral anterior myodome
An	angular
ano	anterior nasal opening (external incurrent nostril)
anpl	angular pit-line
ap	anterior pit-line
apal	articular facet for autopalatine (palate)
apr	anterior process
apsc	posterior ampullary chamber
Ar	articular
art.H	articulation surface for hypohyal
art.Hb	articulation surface for hypobranchial
ascf	anterior scapular foramen
asp	ascending process of parasphenoid
asup 1	articular surface for first suprapharyngobranchial
Aup	autopalatine
Av	accessory vomerine tooth plate
Bb	basibranchial
bhc	bucco-hypophysial canal
bhm	foramen for branches of mandibular nerve to pit organs
binc	tube or foramen for dorsal branch of infraorbital sensory canal in premaxilla; or pore opening therefrom
bpopc	branch of preopercular sensory canal
bpt	basipterygoid process
br	bridge of bone separating V and VII hyomandibular
Bsp	basisphenoid
can	canal through propterygium
can.W	ascending canals of Williamson
Cb	ceratobranchial
cao	aortic canal
cdic	capsule housing diencephalon
Ch	ceratohyal
chy	hyomandibular canal
cla	canal for lateral aorta
Clav	clavicle
Clm	cleithrum
cnc	cavity occupied by nasal capsule
copl	capsule housing optic lobes
Cor	coronoid
cor	canal from orbit to skull roof
corf	coracoid foramen
cotel	canal joining orbit with telencephalon
crd	canal for ascending branch of superficial ophthalmic nerves
csim	cavum sinus imparis
c.sp.	cell spaces
ctel	capsule housing telencephalon
dasc	dorsal opening of anterior semicircular canal
De	dentary
dend	tube or foramen for endolymphatic duct
Dhy	dermohyal
Dmpt	dermometapterygoid
dop	depression for opercular cartilage?
Dpl	dermopalatine
dpl	dentary pit-line
dpsc	dorsal opening of posterior semicircular canal
Dspo	dermosphenotic
dt	dentinal tubules

Eb	epibranchial
Ecpt	ectopterygoid
Enpt	entopterygoid
ep	epural
epi	epineural process
epopc	entrance of preopercular sensory canal
ethc	ethmoidal commissural sensory canal or pit opening therefrom
Exsc	extrascapular
Exsc$_1$	medial extrascapular
Exsc$_2$	lateral extrascapular
fapcv	foramen for anterior tributary of posterior cerebral vein
fbmand.ext.VII	foramen for branches of external mandibular branch of facial nerve
fboca	foramen for branch of occipital artery
fb.IX	foramen for branches of glossopharyngeal nerve to pit-line
fb.X	foramen for branches of vagus nerve to pit-line
fcb	ceratobranchial foramen
fendc	fenestra endonarina communis
fepsa	foramen for efferent pseudobranchial artery
fexna	fenesta exonarina anterior
ffr	fringing fulcra
fhm	hyomandibular facet
fhm.VII	foramen of hyomandibular trunk of facial nerve
fhm.VII + pal	foramen of hyomandibular and palatine trunks of facial nerve
fhy.VII	foramen for hyoid branch of facial nerve
fia	foramen for intersegmental artery
fica	foramen of internal carotid artery
fica$_2$	ascending canal of internal carotid artery in basisphenoid pedicel
fi.Sh	canals for fibres of Sharpey
fm	foramen magnum
fmand.V	foramen for mandibular branch of trigeminal nerve
fmand.VII	foramen for mandibular branch of facial nerve
fmand.int.VII	foramen for internal mandibular branch of facial nerve
fmxv.V buc.VII	foramen for maxillary branch of trigeminal and buccal branch of facial nerve
foa	foramen of orbital artery
foca	foramen of occipital artery
focn	foramen or notch for occipital nerve
fona	foramen of orbitonasal artery
fopa	foramen for ophthalmic artery
for	fenestrae linking dorsal myodomes
fos	otico-sphenoid fissure
fotc	otico-occipital fissure
fotn$_1$	foramen of otic nerve
fpal	foramen of palatine branch of facial nerve
fpal$_2$	entry foramen of palatine nerve into parabasal or palatine canal
Fr	frontal
frd	foramen or notch for ascending branch of superficial ophthalmic nerves
frla	foramen of ramus lateralis accessorius
frla$_1$, frla$_2$	foramen of branch of ramus lateralis accessorius
frmx	foramen for maxillary branch of trigeminal nerve
fst.IX	foramen of supratemporal branch of glossopharyngeal nerve
fv	ventral otic fissure
fvii	venous foramen
g	ganoine
gI	gap in ossification of wall of olfactory nerve canal
gboca	groove for branch of occipital artery
gdend	groove for endolymphatic duct
gf	glenoid fossa
ghm.VII	groove for hyomandibular trunk of facial nerve
gic	groove for internal carotid artery
Gl	lateral gular
gla	groove for lateral aorta
Gm	median gular
gmand.ext.VII	groove for external mandibular branch of facial nerve
goa	groove for orbital artery
goca	groove for occipital artery
gona	groove for orbitonasal artery
gpl	gular pit-line
gpcv	groove for posterior cerebral vein
gph.X	groove or foramen for pharyngeal branch of vagus nerve

gr	groove in dermopalatines and ectopterygoid and in coronoids and prearticular
gst.IX	groove for supratemporal branch of glossopharyngeal nerve
gst.X	groove for supratemporal branch of vagus nerve
g.X	groove for vagus nerve
h$_1$	first hypural
ha	haemal arch
Hb	hypobranchial
hbpt	hole for basipterygoid process
hc	haemal canal
Hh	hypohyal
hll	horizontal longitudinal lamina
hpl	horizontal pit-line
Hy	hyomandibula
Iclav	interclavicle
iepl	insertion points of ethmopalatine ligament
Ih	interhyal
inc	tube or foramen for infraorbital sensory canal or pore opening therefrom
inw	internasal wall
ios	interorbital septum
Ip	infrapharyngobranchial
It	intertemporal
ivl	area of insertion of intervertebral ligament
jc	jugular canal
jg	jugular groove
Ju	jugal
Lac	lachrymal
lapf	fossa for levator arcus palatini muscle
lc	cephalic division of lateral line
lcc	lateral cranial canal
lcom	lateral commissure
ll	foramen through which lateral line enters supratemporal or lateral line scale
lmc	lower muscle canal (= supracoracoid foramen)
lmpt	lamina of metapterygoid
lnabc	lateral nasobasal canal
Men	mentomeckelian
mc	mandibular sensory canal
mcv	foramen of middle cerebral vein
Mk	ossified Meckelian cartilage
mnabc	medial nasobasal canal
mp	middle pit-line
Mpt	metapterygoid
mr	marginal fin-ray
msc	mesocoracoid arch
mscp	mesocoracoid process
mtp	metapterygium
mvfon	margin of vestibular fontanelle
Mx	maxilla
n	notch in margin of supratemporal
Na	nasal
na	neural arch
nabc	foramen of nasobasal canal in floor of nasal capsule
nc	nasal capsule
nfendc	notch for posterolateral part of fenestra endonarina communis
nona	notch for orbitonasal artery
not	notochordal canal
npl	nasal pit-line
oahm	area of origin of adductor hyomandibulae portion of dorsal constrictor
oaop	area of origin of adductor opercularis portion of dorsal constrictor
oatm	area of origin of anterior trunk muscles
oem	area of origin of eye muscles
oexr	area of origin of external rectus muscle
oims$_1$	area of origin of first intermuscular septum
oims$_2$	area of origin of second intermuscular septum
olab	area of origin of levator branchialis muscles
olap	area of origin of levator palatini muscle
Op	opercular
orb	orbit
orc	orbito-rostral canal
Ors	orbitosphenoid
osubc	area of origin of subcephalic muscle
p	pores in premaxilla, nasal and lachrymal
Pa	parietal
pamp	parampullary process
Par	prearticular
parc	opening or course of parabasal canal
pchl	pit for ceratohyal ligament
Pcl	postcleithrum
pdf	posterior dorsal fontanelle
ped	'alisphenoid pedicel'

pesc	posterior opening of external semicircular canal
Pg	pelvic girdle
pinf	pineal foramen
pitf	pituitary fossa
plcc	posterior opening of lateral cranial canal
Pmx	premaxilla
pno	posterior nasal opening (external excurrent nostril)
pnw	postnasal wall
Po	postorbital
po	lateral line pore
podp	pharyngeal (parotic) tooth plate
Pop	preopercular
popc	preopercular sensory canal
por	postorbital process
Pp	postparietal
pp	posterior pit-line
prepf	prepalatine floor
prh	hyoid process of branchiostegal
Pro	prootic
prob	prootic bridge (dorsum sellae)
prof	foramen or canal for profundus nerve
$prof_2$	foramen or canal for branches of profundus nerve
propt	propterygium
Prscl	presupracleithrum
psc	cavity occupied by, or ridge over, posterior semicircular canal
Psp	parasphenoid
Pt	post-temporal
Pts	pterosphenoid
pu8	eighth pre-ural centrum
pv	foramen or pathway for pituitary vein
Qu	quadrate
Quj	quadratojugal
qujpl	quadratojugal pit-line
r	radial
rbuc	buccal nerve
Rbr	branchiostegal ray
rcor	coracoid ridge
rdo	ascending branches of superficial ophthalmic nerves
rhm+pal	hyomandibular trunk and palatine branch of facial nerve
rla	ramus lateralis accessorius
rmet	recess housing metencephalon
rmye	recess housing myelencephalon
Ro	rostral
ropl	recess housing optic lobe
rot	otic nerve
rpl	radial plate
rsoc	recess on roof of otic region
rtel	recess housing telencephalon
sacr	saccular recess
San	supra-angular
sc	scale
scf	scapular or coracoid foramen
Scl	supracleithrum
sgf	supraglenoid foramen
sn	supraneural
Soc	supraoccipital
Sop	subopercular
Sp	suprapharyngobranchial
sp	spiracular opening
spic	spiracular bar
spig	spiracular groove
spip	spiracular tooth plate
ssu	division of labyrinth cavity for the sinus superior
St	supratemporal
stc	supratemporal commissural sensory canal
suc	tube or foramen for supraorbital sensory canal or pore opening therefrom
svfotc	sub-vagal portion of otico-occipital fissure
svr	recess housing saccus vasculosus
Tab	tabular
tp	toothplate
utr	utricular recess
va	ventral arch
vfon	vestibular fontanelle
vnabc	ventral nasobasal canal
vnabcf	opening of ventral nasobasal canal in roof of mouth
Vo	vomer
vpl	vertical pit-line
Z	zygal plate
I	tube or foramen for olfactory tracts

II	optic fenestra	VI_1, VI_2	foramina of abducens nerve
III	notch, foramen or canal of oculomotor nerve	VII	foramen or canal for facial nerve
IV	notch or foramen of trochlear nerve	VII.lat	foramen or canal for lateralis trunk of facial nerve
V	foramen or canal for trigeminal nerve	IX	foramen of glossopharyngeal nerve
VI	foramen of abducens nerve	X	foramen of vagus nerve

Systematic descriptions

Family **STEGOTRACHELIDAE** Gardiner, 1963

Genus ***MIMIA*** Gardiner & Bartram, 1977

Diagnosis. Stem-group actinopteran fishes in which the ventral otic fissure passes into the rear of the orbit; the parasphenoid is broad but without basipterygoid or ascending processes; the otico-sphenoid fissure is cartilage-filled; a pair of orbitonasal arteries passed into the orbit immediately lateral to the ventral otic fissure; the spiracular groove is wide, there is a spiracular slit between intertemporal and dermosphenotic; the neurocranium contains a lateral cranial canal; the perforated pectoral propterygium is embraced by the bases of the marginal rays; and basal and fringing fulcra are present.

Type species. *Mimia toombsi* Gardiner & Bartram, 1977.

Remarks. *Mimia* and *Moythomasia* are closely related Devonian fishes which have been placed in the family Stegotrachelidae (Gardiner 1963; Gardiner & Bartram 1977). Unfortunately all the characters they share with *Stegotrachelus* are primitive, but until we know more of the internal anatomy of *Stegotrachelus* and other stem-group actinopterans it is premature to suggest alternative family groupings. Consequently the genera will be referred to either as *Mimia* and *Moythomasia* or as 'the Gogo palaeoniscids' in the following account.

Mimia toombsi Gardiner & Bartram, 1977

1970 Devonian stegotrachelid; Gardiner: 285; fig. 3.
1971 Stegotrachelid palaeoniscoid; Gardiner *in* Moy-Thomas & Miles: figs 5, 6.
1973 Gogo palaeoniscid 'A'; Gardiner: 106; figs 1, 2, 6, 8, 9.
1973 Gogo palaeoniscid 'B'; Gardiner: figs 3, 4.
1975 Gogo palaeoniscid; Gardiner & Miles: fig. 2.
1977*b* Palaeoniscoid; Patterson: fig. 1B.
1977 *Mimia toombsi* Gardiner & Bartram: 228; figs 1–6.

Diagnosis. As for genus.

Holotype. Western Australian Museum 70.4.245; partly disarticulated specimen wanting fins, in counterpart, from the Upper Devonian, Gogo Shales, Gogo Station (H.A.T. 67/80, see Miles 1971*b*), Fitzroy Crossing, W. Australia.

Specimens. This study is based on 61 specimens from the following Gogo localities: 21, 25, 27, 30, 36, 37, 42, 47, 54, 55, 56, 63, 73, 80, 84, 87, 89, 91, 92, 302 (for Gogo localities see Miles 1971*b*: fig. 1).

Genus ***MOYTHOMASIA*** Gross, 1950
[= *Aldingeria* Gross 1942:431]

Diagnosis. See Gross (1942: 430) and Jessen (1968: 89). In addition the ventral otic fissure passes into the rear of the orbit; the parasphenoid is broad with a rudimentary ascending process but no basipterygoid process; the palatoquadrate has a short anterior process; there is a spiracular slit between the intertemporal and dermosphenotic and the dermosphenotic is hinged to the jugal as in *Mimia* and *Cheirolepis*; the neurocranium has a lateral cranial canal; the lower jaw has a supra-angular; the pectoral fin has a perforated propterygium embraced by the bases of the marginal rays; there are prominent basal fulcra above and below tail; and fringing fulcra are present on all fins.

TYPE SPECIES. *Moythomasia perforata* (Gross).

REMARKS. The genus is known from the Devonian (Frasnian) of Kokenhusen, Latvia, Bergisch Gladbach and Wildungen, Germany and Gogo, Western Australia (Gross 1950, 1953; Jessen 1968; Gardiner & Miles 1975; Gardiner & Bartram 1977).

Moythomasia durgaringa Gardiner & Bartram, 1977

1973 Gogo palaeoniscid 'B'; Gardiner: figs 5 and 7 only (not figs 3, 4).
1977 *Moythomasia durgaringa* Gardiner & Bartram: 238; fig. 7.
1981 *Moythomasia durgaringia* Gardiner & Bartram; Forey & Gardiner: 140.

DIAGNOSIS (emended). A *Moythomasia* with scales with up to 15 serrations posteriorly.

HOLOTYPE. Western Australian Museum, 70.4.244; partly disarticulated head and body in counterpart from the Upper Devonian, Gogo Shales, Gogo Station (H.A.T. 67, see Miles 1971*b*), Fitzroy Crossing, W. Australia.

SPECIMENS. This study is based on 18 specimens from the following Gogo localities: 36, 37, 72, 78, 80, 84, 86, 89.

Neurocranium: general features

The neurocrania of *Mimia* and *Moythomasia* are very similar, more or less completely ossified, with both external and posterior semicircular canals visible externally.

Comparative measurements show that in both the maximum breadth (between the postorbital processes) is about 60% of the total length, while the depth, which remains remarkably constant throughout, is some 34% of the length. The orbital length (postorbital process to tip of ethmoid) constitutes at least 55% of total braincase length in *Mimia*, but in *Moythomasia* the orbital length is 50% of total braincase length.

Although the neurocrania are, for the most part, both perichondrally and endochondrally ossified, the degree of ossification is greater posteriorly. Thus the greatest thickness of endochondral bone occurs around the tip of the notochord (in the area of the prootic bridge) and there is little endochondral bone in front of the basipterygoid process ventrally or the pineal foramen dorsally. Well-developed endochondral bone is confined to the postorbital portion of the braincase and that area around the hypophyseal foramen (including the basipterygoid process). In this respect it is interesting to note that ossification of the osteichthyan skull commences around the notochordal plate and proceeds anteriorly. The whole of the preorbital regions of the neurocrania of *Mimia* and *Moythomasia* are only perichondrally ossified, while in front of the basipterygoid processes up to the anterior limits of the orbits endochondral bone can only be recognized in thin section as mere wisps of tissue in the more lateral areas of the neurocranial ossifications. In presumed younger individuals the area anterior to the nasal capsules is often not even perichondrally ossified; only in a few mature individuals does a complete layer of perichondral bone occur.

The anterior region of the neurocrania of *Mimia* and *Moythomasia* is thus only perichondrally ossified. In this respect they resemble some of the pholidophorid and leptolepid neurocrania described by Patterson (1975: 473), of which he remarked 'the ethmoid region is often missing from the fossils, and when preserved is as a rule less thoroughly ossified'; he added that the ethmoid area is frequently only perichondrally ossified. Although the ethmoid region is as a rule less thoroughly ossified in primitive actinopterygians (cf. *Pteronisculus* Nielsen 1942, *Birgeria* Nielsen 1949, *Kansasiella* Poplin 1974), in the majority of other fossil osteichthyans this region is invariably endochondrally ossified (*Nesides* Stensiö 1932*b*, *Eusthenopteron* Jarvik 1954, *Glyptolepis* Jarvik 1972, *Chirodipterus* Säve-Söderbergh 1952, *Griphognathus* Miles 1977).

From what evidence is available it appears that the neurocranium of chondrichthyans, acanthodians and placoderms is composed solely of perichondral bone. If the Actinopterygii are the sister-group of the Sarcopterygii (Rosen *et al.* 1981) then the absence of endochondral bone in the snout of early actinopterygians is probably a primitive feature.

The endochondral bone, where it occurs in the neurocrania of *Mimia* and *Moythomasia*, is thick and cancellate with large medullary spaces surrounded by delicate laminae, and with external and internal surfaces and all canals for vessels or nerves lined with thin, laminate, perichondral bone which shows few traces of radial structures; consequently it is difficult to deduce individual ossification centres. In this they resemble many fossil actinopterygians including palaeoniscids, perleidids, pholidopleurids, parasemionotids (Nielsen 1942, 1949) and pholidophorids (Patterson 1975: 288).

While separate ossifications are not evident in the neurocrania of many primitive actinopterygians, there are several notable exceptions. Discrete oss*ifications have been described in the palaeoniscids Cosmoptychius* (Watson 1928: 49), *Pteronisculus magnus* (Nielsen 1942) and *Birgeria* (Stensiö 1921, Nielsen 1949), in *Perleidus* cf. *stoschiensis* (Patterson 1975: 456), and in the living *Polypterus, Acipenser* and *Polyodon* (see Patterson 1975: 463 for summary). Elsewhere within the actinopterygians ossification centres are also recognizable in parasemionotids (Lehman 1952: 162, Patterson 1975: 432), caturids such as '*Aspidorhynchus*' (Rayner 1948: 315, Patterson 1975: 436), *Macrepistius* (Schaeffer 1971) and *Caturus furcatus* (Patterson 1975: 441), and in the amiids *Enneles* (Santos 1960), *Sinamia* (Stensiö 1935) and the extant *Amia*. They have also been described in the semionotids *Lepidotes* (Woodward 1916, Patterson 1975: 449) and the living *Lepisosteus*, in the pachycormids *Pachycormus* (Rayner 1948, Patterson 1975: 443), *Hypsocormus* (Stensiö 1935) and *Protosphyraena* (Loomis 1900, Lehman 1949), in the Mesozoic pholidophorids and leptolepids (Patterson 1975) and in most Recent teleosts.

In all the specimens of *Mimia* and *Moythomasia* examined the braincase was fully ossified and sutureless, yet some specimens of *Moythomasia* are only a third the size of others. Patterson (1975: 287) observed a similar size discrepancy in the ossified neurocrania of *Pholidophorus bechei*, so presumably as in *Pholidophorus* ossification in *Mimia* and *Moythomasia* must have set in early in ontogeny and growth have been terminated by fusion of the bones.

However, the absence of separate ossifications in the neurocrania of Devonian actinopterygians and most of the known primitive fossil actinopterygians, and the presence of separate bones in later actinopterygians, can be accounted for by two hypotheses. The neurocranium may have ossified primitively in a single piece and in subsequent evolution have fragmented into several ossification centres, independently in different lines (Stensiö 1932*b*: 297). Alternatively the neurocranium may always have ossified from a discrete set of centres, in more primitive forms growth being thus terminated by fusion of the constituent bones, whereas in others the sutures remained open to allow persistent growth, as in living teleosts (Gardiner 1960: 359, Schaeffer 1971: 21, Patterson 1975: 288). Elsewhere discrete endocranial bones are found in *Acanthodes* (Miles 1971*a*), *Ctenurella* (Miles & Young 1977), all post-Devonian actinistians (and possibly even *Nesides* in which the back of the skull is missing), *Eusthenopteron* (Stensiö 1932*b*: 297, Jarvik 1972) and tetrapods. Separate bones have also been described in the Devonian dipnoan *Dipnorhynchus* (Campbell & Barwick 1982), but with the exception of the exoccipitals of *Neoceratodus* no separate ossifications have ever been noted in Recent dipnoan neurocrania. In shark neurocrania perichondral bone develops at the surface of the individual tesserae (Kemp & Westrin 1979) and there are therefore numerous ossification centres.

If the phylogenetic fragmentation hypothesis is correct then fragmentation must have occurred on at least five separate occasions: within the chondrichthyans, within the acanthodians, within the placoderms, within the actinopterygians and once again within the remaining osteichthyans. This hypothesis is thus extravagant, and since the endochondral bone of the braincase in all Recent gnathostomes grows from a suite of fixed centres it is difficult to believe that in the braincase of Devonian fishes endochondral (and perichondral for that matter) bone grew in some as yet undescribed fashion. Consequently, I am forced to continue to support the non-fragmentation hypothesis of braincase ossification, in which it is proposed that the neurocranium always ossified from a discrete set of centres.

Unfortunately, this hypothesis has been further complicated in actinopterygians by two additional, conflicting hypotheses, either that there has been an increase of ossification centres ('fragmentation'), or that there has been an decrease ('fusion', loss). But, as Patterson (1975: 470) points out, most of the evidence in support of a subdivided neurocranium being the derived condition rests on the assumption that teleosts possess the most highly subdivided neurocrania. Patterson (1975: 470) has however clearly demonstrated that the braincase of living teleosts contains fewer endochondral bones than the more primitive pholidophorids, and they certainly contain fewer bones than early pachycormids (personal observation). From his survey of braincases Patterson (1975) has shown that 'the dominant process in actinopterygian evolution has been reduction in the number of endocranial ossifications, not increase . . . examples of loss being numerous especially in the pholidophorids and teleosts'.

Other evidence for the fragmentation hypothesis rests on the observations that in *Polypterus* and in palaeoniscids, where ossification patterns are known (*Cosmoptychius* and *Birgeria*), there are fewer bones than in teleosts and many halecomorphs, while the Permian *Acanthodes* has a pattern of neurocranial bones similar to *Cosmoptychius*. Patterson (1975: 465) has demonstrated that the conditions in *Polypterus* and *Birgeria* are similar and that they both differ considerably from the palaeoniscid type from which they can most reasonably be derived by assuming loss of ossifications.

Cosmoptychius (Watson 1928, Schaeffer 1971) on the other hand is known from but a single, incomplete specimen. It is similar in many respects to some of the smaller skulls of *Moythomasia* and, as Patterson (1975: 402) commented, is probably composed of the same series of bones as in most palaeoniscids. The fact that there is but one large paired ossification, one small median ossification and two pairs of smaller ossifications in this specimen is not evidence that the braincase ossified from the same number of centres. Thus, the occipital ossification probably included basi- and exoccipitals as well as an intercalar, and the upper part of the occiput, which is missing from the specimen, must have included epioccipitals.

Finally the pattern of ossification in *Acanthodes* is superficially actinopterygian-like and said to resemble that in *Cosmoptychius* (Schaeffer 1971, Miles 1973*a*). But the braincase of *Acanthodes* (Miles 1971*a*: fig. 4·7) differs from most actinopterygians in not possessing either epioccipitals or prootics and in not having endochondral ossification. It is also possible (Denison 1979) that the condition in *Acanthodes* (the last of the acanthodians) is not primitive for acanthodians and that *Acanthodes*, like the living chondrosteans and *Polypterus*, may have lost several ossification centres.

The conclusion which may be drawn from this discussion is that the hypothesis of loss of neurocranial ossification centres has more to support it than the conflicting hypothesis of increase of centres by fragmentation. It follows from the acceptance of this conclusion that the common ancestor of the gnathostomes possessed a neurocranium which ossified from a number of centres and that the number of centres in chondrichthyans is far greater than in the rest of the gnathostomes. Furthermore the pattern of ossification seen in chondrichthyans is different from that in other gnathostomes. In chondrichthyans the prismatic calcifications remain tesserate throughout life and the cap zone of the individual tesserae forms a thin veneer of perichondral bone; growth is accomplished by enlargement of the individual prisms (Kemp & Westrin 1979). In osteichthyans the ossification centres are far fewer, ossification commences as a disc on the surface of the cartilage model and the sutures may remain open so that growth is continuous.

Within the various non-chondrichthyan lineages loss of neurocranial ossification centres has occurred independently, maybe in relation to varying mechanical factors such as neurokinesis etc., and until the phylogenetic homologies have been worked out for each group we can only presume that topographically similar bones in the neurocrania of acanthodians, actinopterygians, actinistians, rhipidistians and tetrapods are not necessarily homologous.

Miles (1977) has recently argued that the presence of endochondral bone in the snout of the Devonian dipnoan *Griphognthus* is primitive in relation to the condition in other Devonian dipnoans such as *Chirodipterus* and *Holodipterus*, where endochondral bone is restricted to the otic and occipital regions. But if, as argued above, endochondral bone is primitively absent from the snout of actinopterygians, and the actinopterygians are the sister-group of the remaining osteichthyans (Gardiner 1973, Rosen *et al.* 1981), then it is more likely that the condition of the snout of *Griphognathus* is specialized in respect to *Chirodipterus* and *Holodipterus*.

In order to substantiate the argument that endochondral bone is primitively absent from the snout of actinopterygians it is necessary to re-examine the occurrence of endochondral bone in early vertebrates.

Some authors (Miles 1977, Schaeffer 1971) consider perichondral and endochondral bone to be of equal antiquity and also primitive for all bony vertebrates. There is little doubt that perichondral bone, like dermal bone, is a primitive vertebrate tissue since both occur in cephalaspids (Stensiö 1927, 1932*a*), placoderms (Stensiö 1963*a, b*), acanthodians, bony fishes and tetrapods. On the other hand endochondral bone has a more limited distribution. In the whole of the Agnatha the only record of endochondral bone is in the cephalaspid *Boreaspis* (Wängsjö 1952: fig. 1). Re-examination of Wängsjö's thin section of *Boreaspis* has convinced me that this is merely an extensive perichondral ossification similar to that seen in thin sections of other cephalaspids. It is worth noting that in mammals growth of a perichondral ossification may result in replacement of the entire cartilage that it envelops, and that in very weakly ossified neurocrania, such as that of the chondrostean *Polyodon*, the bones consist merely of scale-like perichondral ossifications.

Through the kindness of Dr G. Young I have had the opportunity of examining several neurocrania of Devonian placoderms from Australia including *Brindabellaspis stensioi* Young, *Buchanosteus confertituberculatus* (Chapman) and *Wijdeaspis warrooensis* Young; all show extensive perichondral ossifications but none shows any trace of endochondral bone. Recently Miles & Young (1977: 168; fig. 21) have stated that in one specimen of the ptyctodontid *Ctenurella gardineri* Miles & Young endochondral bone is present in the ethmoidal bone. Re-examination of this specimen (BMNH P.57665) convinces me that what they termed endochondral bone is probably calcified cartilage. If placoderms lack endochondral bone and are more closely related to chondrichthyans than to other gnathostomes (Miles & Young 1977), or are the sister-group of osteichthyans, then endochondral bone must be considered a specialization of osteichthyans, as Rosen *et al.* (1981) presumed, and the absence of endochondral bone from the snout of Devonian actinopterygians and dipnoans is a primitive character.

Occipital region

The neurocrania of *Mimia* and *Moythomasia* are ossified in a single piece as in the palaeoniscids *Boreosomus* (Nielsen 1942), *Pteronisculus macropterus* (Beltan 1968) and *Kansasiella* (Poplin 1974); consequently individual bones are not apparent and it is not easy to delimit regions, except in a very general way. Here the occipital region is taken to be that area of braincase behind the occipital fissure (fissura otico-occipitalis) and below the vestibular fontanelle and extending anteriorly as far as the ventral otic fissure (fissura oticalis ventralis).

Mimia toombsi

Dorsally the occipital region is separated from the otic by a small, oval posterior dorsal fontanelle (Pl. 1; pdf, Figs 26, 79). This represents the expanded dorsal portion of the occipital fissure. The posterior dorsal fontanelle is smaller than that in *Kansasiella* (Poplin 1974: fig. 12), *Pteronisculus* (Nielsen 1942: fig. 7), *Australosomus* (Nielsen 1949: fig. 3) and *Kentuckia* (Rayner 1951: fig. 6), and is lined throughout with perichondral bone. Although this fontanelle is also perichondrally lined in *Australosomus* (Nielsen 1949: 27) there is no perichondral lining in *Pteronisculus* (Nielsen 1942: 41) and presumably it was cartilage-filled. The fontanelle is closed by bone in some specimens of *Boreosomus* whereas in others it remains open (Nielsen 1942: 287).

The occipital fissure (fotc, Figs 4, 5, 6, 12, 13, 15, 50), which represents the persistent metotic fissure between the occipital arch and otic capsule of the embryo, passes anteroventrally from

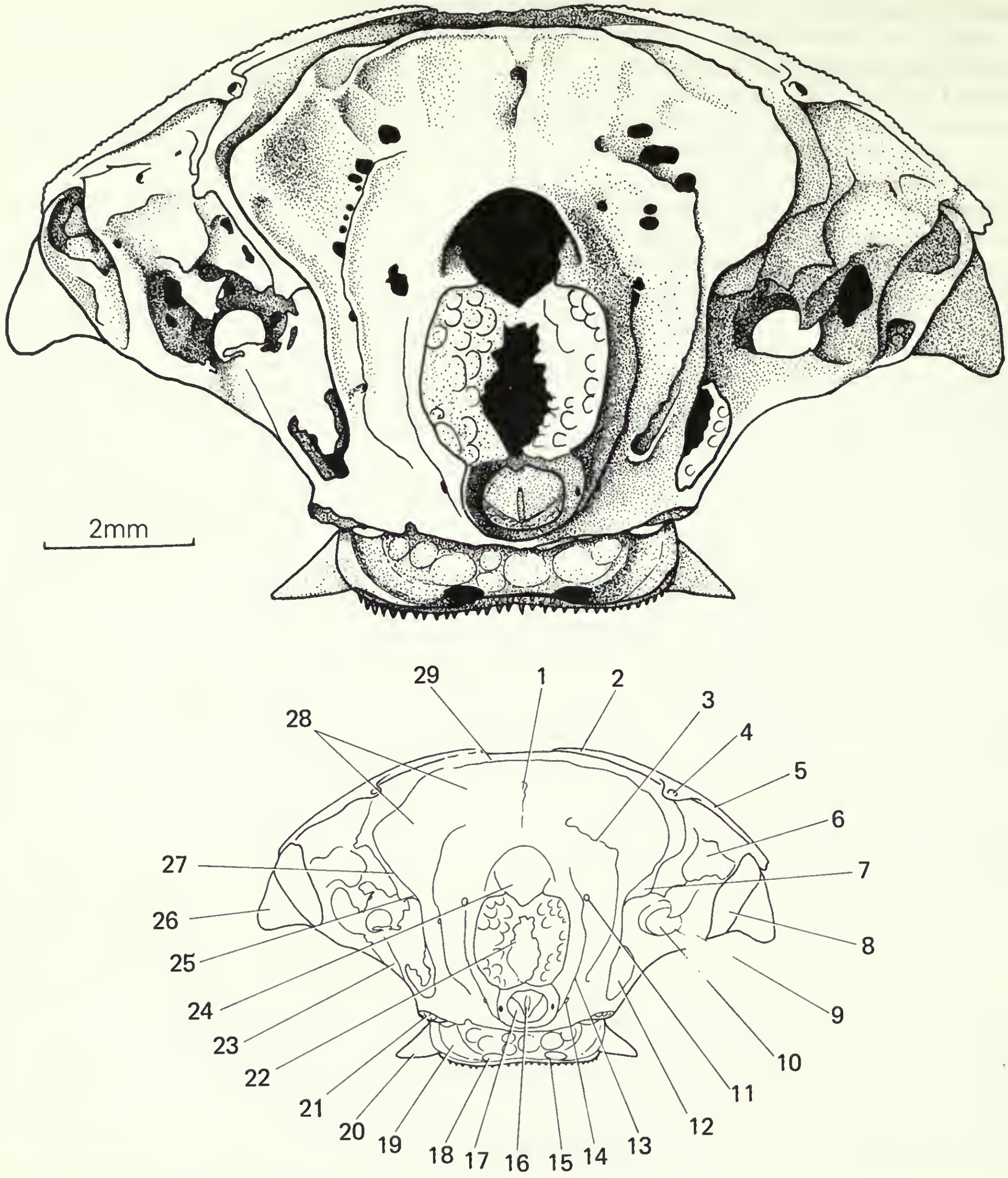

Fig. 1 *Mimia toombsi* Gardiner & Bartram. Neurocranium and attached dermal bones in posterior view, basisphenoid displaced ventrally; from BMNH P.56504. Key (diagram below): 1, ivl; 2, Pa; 3, $oims_1$; 4, ll; 5, St; 6, oahm + oaop; 7, apsc; 8, fhm; 9, ghm.VII; 10, jc; 11, focn; 12, vfon; 13, $oims_2$; 14, foca; 15, Psp; 16, alig; 17; cao; 18, fica; 19, gona; 20, bpt; 21, aip 1; 22, not 23, goa; 24, fm; 25, X; 26, por; 27, fotc; 28, oatm; 29, pdf. For explanation of lettering used on text-figures, see pp. 177–181.

the posterior dorsal fontanelle to terminate in an ovoid vestibular fontanelle. The vestibular fontanelle (vfon, Figs 1, 5, 13, 14, 15, 50) has no perichondral lining and was presumably cartilage-filled. It represents an area between adjacent ossifications (opisthotic, basioccipital and prootic ossifications deduced from Patterson 1975: 461) and is one of the few areas of the braincase which remains unossified in the adult early osteichthyan.

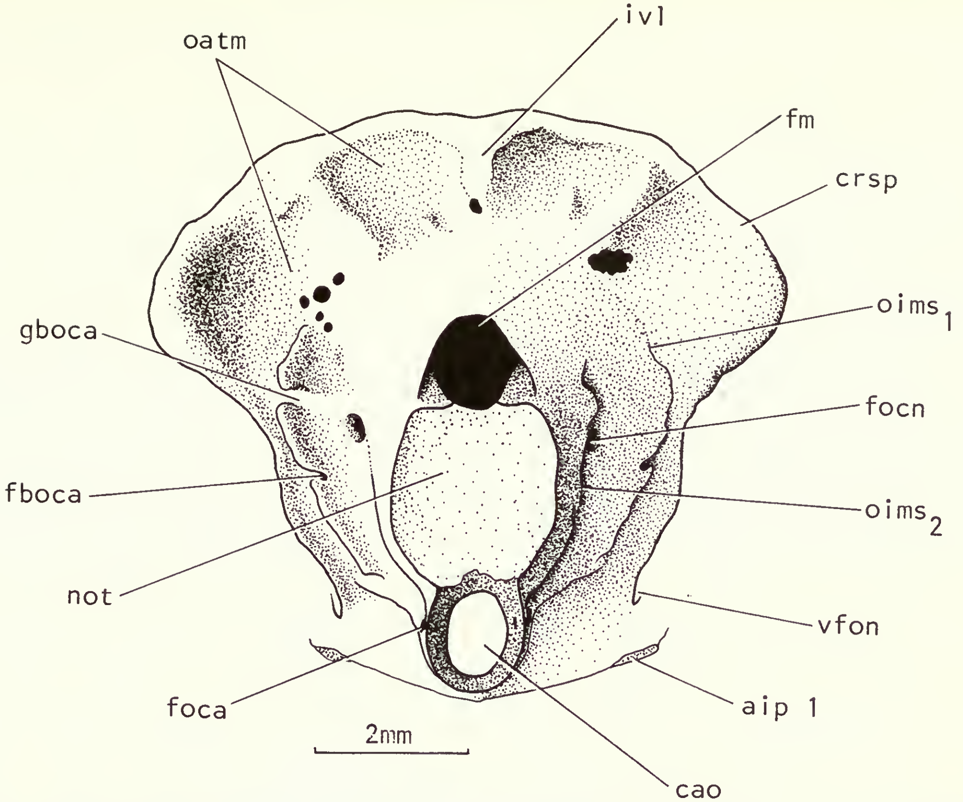
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Fig. 2 *Mimia toombsi* Gardiner & Bartram. Occipital ossification in posterior view, from BMNH P.53243.

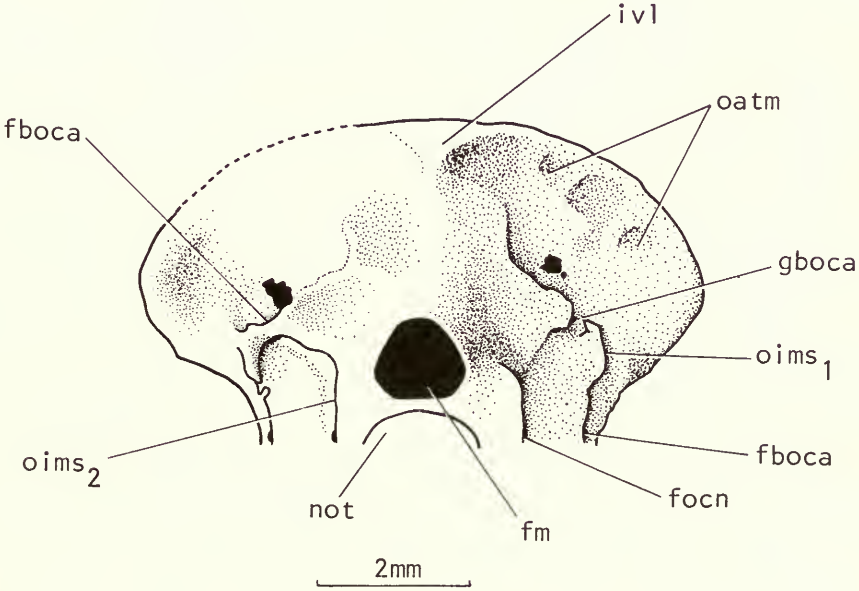
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Fig. 3 *Mimia toombsi* Gardiner & Bartram. Dorsal part of the occipital ossification in posterior view, from BMNH P.56496.

The vestibular fontanelle of *Mimia* is somewhat smaller than in *Kansasiella* (Poplin 1974: fig. 13) and much smaller than in either *Kentuckia* (Rayner 1951: fig. 7) or *Pteronisculus* (Nielsen 1942: fig. 4). In size and shape it is quite similar to that in *Pholidophorus bechei* (Patterson 1975: fig. 56).

In early, less specialized, palaeoniscids the occipital fissure is complete and perichondrally lined throughout, except in *Moythomasia* (see p. 201 and Figs 8, 9), where a small area above the upper margins of the vagus canal lacks perichondral bone, and in some individuals of *Boreosomus piveteaui* (Nielsen 1942: fig. 59) where the mid-dorsal part of the fissure may be closed by a narrow bridge of bone. In other later, more advanced palaeoniscids such as *Birgeria* (Nielsen 1949: 190) the perichondral lining is missing and the fissure is presumably already cartilage-filled.

Anteriorly the occipital region in *Mimia* is bounded by another, completely separate fissure, the ventral otic fissure. This fissure (fv, Figs 13, 14, 15, 16, 22, 26, 50) lies in the floor of the neurocranium and passes up immediately behind the foramen for the pituitary vein and anterior to the foramen for the abducens nerve. The fissure is not perichondrally lined and was cartilage-filled in life; it represents the cartilage remaining between ossifications in the trabeculae (+polar cartilages) and parachordals, and must represent the gap between the chordal and prechordal skeleton of the embryo. The fissure separates the basioccipital from the basisphenoid (ossifications deduced from Patterson, 1975) in the mid-line and from the prootics

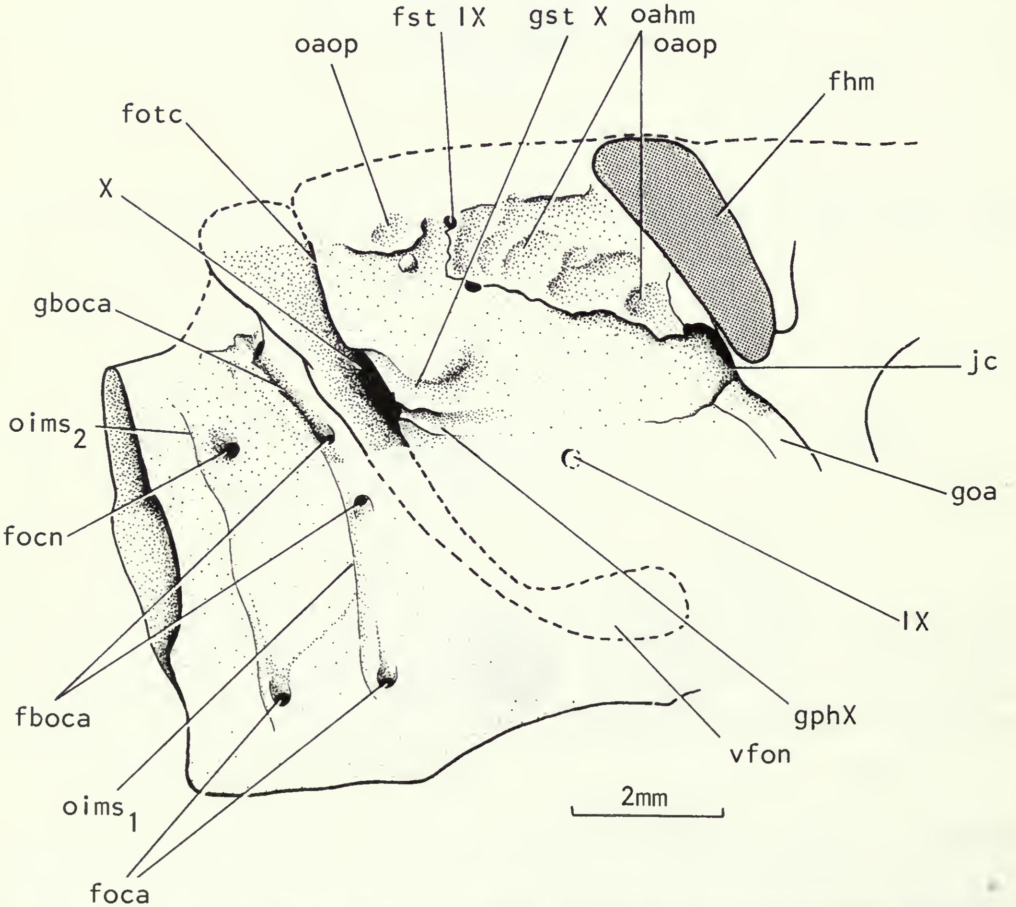

Fig. 4 *Mimia toombsi* Gardiner & Bartram. Otic and occipital regions in right lateral view, from BMNH P.56501.

dorsolaterally. From the floor of the neurocranium the fissure passes up behind the 'prootic' bridge to open into the front of the notochordal canal (not, Figs 25, 26). Laterally, at the level of the presumed junction between the basioccipital and prootics, the ventral otic fissure gives way on either side to a large foramen for the orbitonasal artery (fona, Figs 15, 50).

In the Gogo palaeoniscids the ventral otic fissure is therefore situated below the hind wall of the orbit and well in front of the vestibular fontanelle, from which it is separated by the bony wall of the neurocranium (the prootic and basioccipital). The ventral otic fissure is also separated from the vestibular fontanelle in other palaeoniscids such as *Kansasiella* (Poplin 1974: figs 13, 14), *Pteronisculus macropterus* (Beltan 1968: fig. 2) and *Boreosomus* (Nielsen 1942: fig. 63).

Although the limits of the individual ossifications making up the occipital region cannot be made out with certainty because in most cases individual sutures are absent, in some specimens and in certain areas ossification centres can be determined with considerable confidence. In all specimens of the Gogo palaeoniscids the floor and roof of the notochordral canal (and neurocranial floor) are incompletely ossified in the mid-line posteriorly, and in one specimen of *Mimia* (BMNH P.53250) there is a median suture running the whole length of the floor of the notochordal canal from the ventral otic fissure to the posterior limit of the neurocranium. This obviously paired ossification in the floor of the braincase must be the basioccipital. Elsewhere in osteichthyans (including tetrapods) the basioccipital is usually a median ossification (except perhaps for *Polypterus* and *Pachycormus*; Patterson 1975: 445, 448), but its origin must have been from paired ossification centres in the parachordal cartilages. Interestingly the basioccipital of *Acanthodes* (Miles 1973*a*: fig. 11) is incised in the mid-line both anteriorly and posteriorly and this is taken to indicate the paired origin of that perichondral bone. In front of the foramen magnum the basioccipital forms the floor of the neurocranium, the floor and lateral walls of the notochordal canal (see Fig. 25) and the ventral and posterior margins of the vestibular fontanelle. Anterolaterally the basioccipital passes indistinguishably into the prootics. The basioccipital fails to meet in the mid-line posteriorly beneath the notochordal canal in several other palaeoniscids, thus the notochordal canal is contiguous with the aortic canal in *Pteronisculus* (Nielsen 1942: 32), *Kansasiella* (Poplin 1974: figs 11, 20), *Boreosomus* (Nielsen 1942: fig. 61) and *Cosmoptychius* (Schaeffer 1971).

The roof of the notochordal canal and the floor of the foramen magnum is made up by another pair of ossifications, the exoccipitals. This can be recognized because the ossification centres for these bones in other osteichthyans lie lateral and somewhat ventral to the floor of the foramen magnum, and because, although the foramen magnum is completely lined with bone dorsally and laterally, the ossifications do not always meet in the mid-like posteroventrally (see *Moythomasia*, Figs 8, 9, 10). A posterior notch in the floor of the foramen magnum in *Pteronisculus* (Nielsen 1942: 32) and *Kansasiella* (Poplin 1974: fig. 14) represents this unossified area in the Gogo palaeoniscids.

The upper margin of the occipital arch is occasionally produced anteriorly, partly closing the fontanelle, and this may represent a median supraoccipital. The extent of the supraoccipital is very uncertain in most specimens of *Mimia*, but can be more clearly discerned in *Moythomasia* (see Fig. 10). While there is no evidence of a supraoccipital in *Pteronisculus* (Nielsen 1942: fig. 7), *Kentuckia* (Rayner 1951: fig. 6) and *Australosomus* (Nielsen 1949: fig. 3), a median protuberance in *Kansasiella* (Poplin 1974: fig. 12; av.) and the closure of the posterior dorsal fontanelle in *Boreosomus* (Nielsen 1942: 286) support the idea that such a bone existed in these last-named forms at least. Elsewhere in primitive actinopterygians a supraoccipital is possibly present in *Perleidus* (Patterson 1975: 456), where its presence is inferred from the mode of closure of the uppermost part of the occipital fissure (posterior dorsal fontanelle).

The occipital region occupies less than 15% of the total neurocranial length measured through the vagus foramen and in this respect *Mimia* is similar to *Pteronisculus* (Nielsen 1942: fig. 4) and *Kansasiella* (Poplin 1974: fig. 13). The occipital region is much shorter in the pholidopleurid *Australosomus* (Nielsen 1949: fig. 2) and in the primitive teleost *Pholidophorus* (Patterson 1975: fig. 56). The occipital region is not as deep as the rest of the neurocranium, the greatest depth being attained immediately in front of the ventral otic fissure, much as in *Boreosomus* (Nielsen 1942: fig. 62).

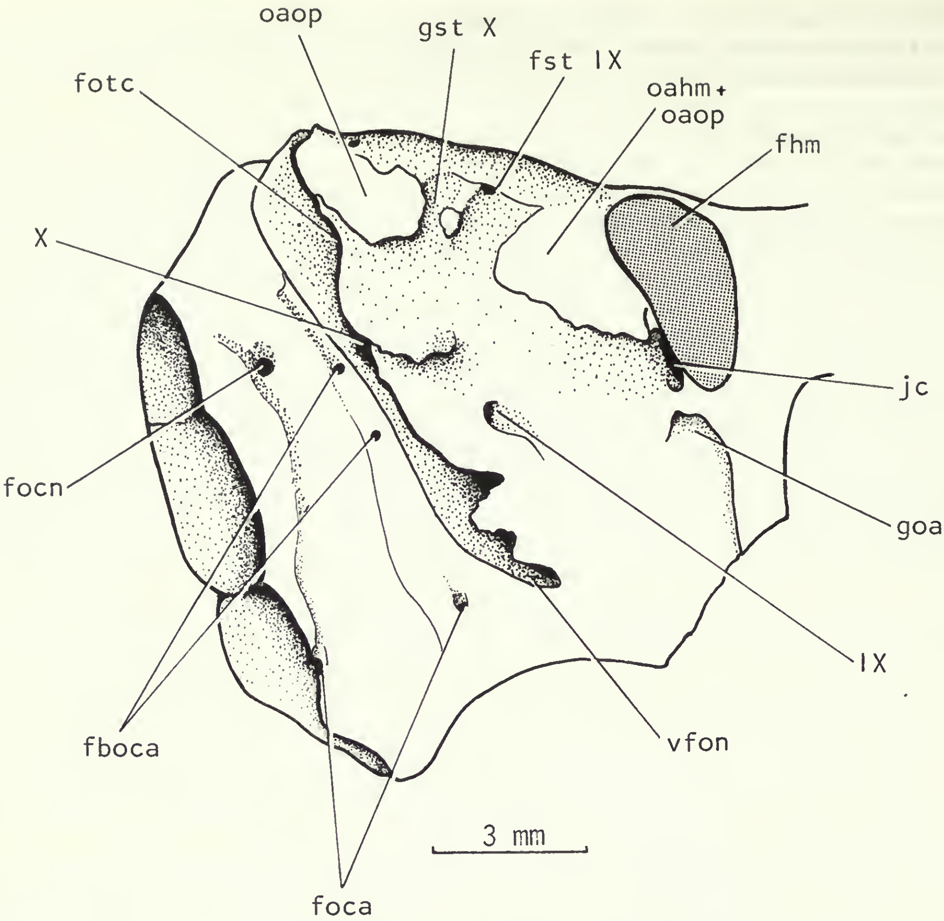

Fig. 5 *Mimia toombsi* Gardiner & Bartram. Otic and occipital regions in right lateral view, from BMNH P.53234.

The posterior face of the occiput (Figs 1, 2, 3) is broader above the foramen magnum than below, and the dorsal margin is gently rounded. The greatest width is at the level of the dorsal margin of the formen magnum where the outline is more acutely rounded before the bone turns increasingly forwards and inwards to merge into the ventral surface. An acutely rounded dorsolateral prominence (Fig. 2) is assumed to be made up by the intercalar. This lies immediately posterodorsal to the vagus foramen and has been termed the cranio-spinal process by Nielsen (1942: 38). It is homologous with the cranio-spinal process in other palaeoniscids and chondrosteans such as *Saurichthys, Acipenser* and *Polydon*. Patterson (1975: 315) has shown that the intercalar in *Pholidophorus* is the homologue of the cranio-spinal process of chondrosteans but here, as in halecostomes, it received the ligament from the ventral limb of the post-temporal. No such ventral limb existed in palaeoniscids and there is no evidence of a ligament; there is likewise no such limb in chondrosteans though an extension from the post-temporal in *Acipenser* reaches the occipital process posterior to the vagal foramen (Jollie 1980: 240). (A limb does exist in *Polypterus* but this is inferred to have arisen independently of that in neopterygians). The cranio-spinal process is also found in acanthodians (Miles 1973*a*: 86) and placoderms (Stensiö 1969; Young 1980: fig. 8, infravagal process) and may be a primitive gnathostome attribute. Miles (1977: 55) has suggested that either the transverse process in dipnoans may be homologous with the cranio-spinal process, or it may be serially homologous

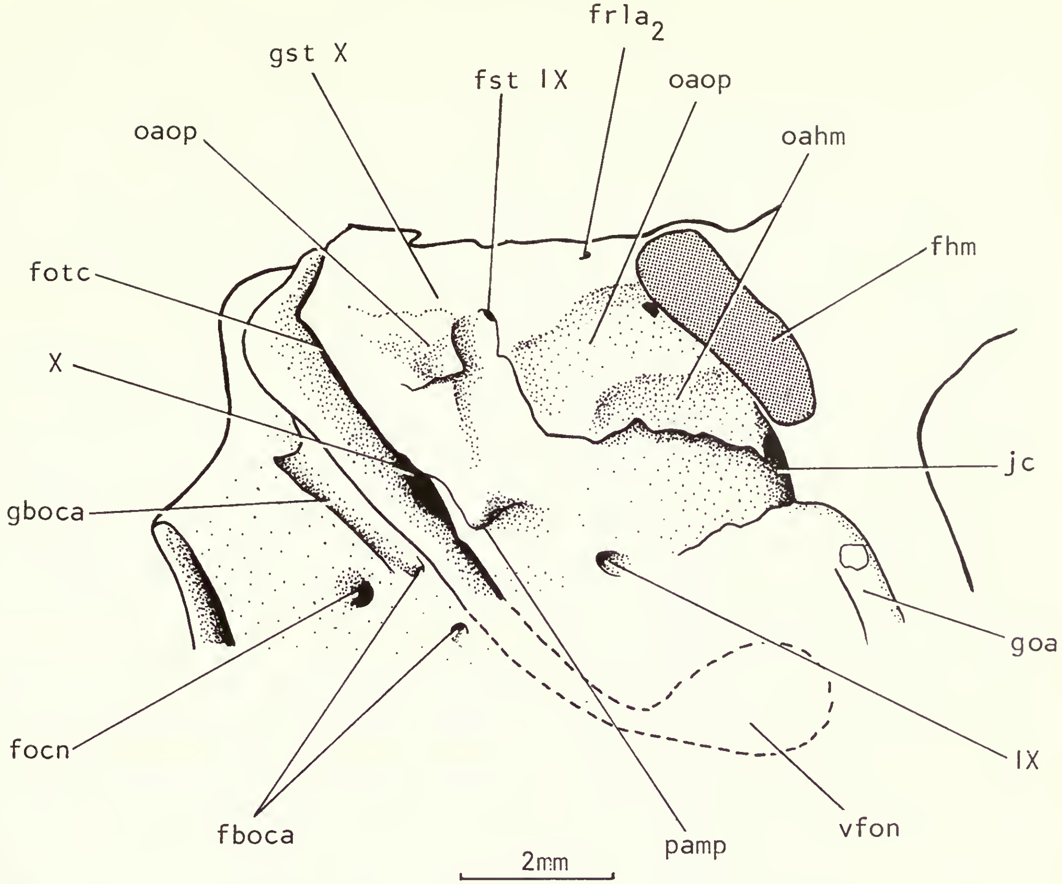

Fig. 6 *Mimia toombsi* Gardiner & Bartram. Dorsal portion of the otic and occipital regions in right lateral view, from BMNH P.56496.

with it if the cranio-spinal process represents an epineural. The first suggestion is unlikely since the intercalar lies in front of the first intermuscular septum in *Mimia* and forms part of the posterior margin of the occipital fissure as well as the hind margin of the foramen for the vagus nerve, whereas in fossil dipnoans the transverse process lies behind the third occipital nerve and so is quite distant from the vagus foramen and the occipital fissure. Separate epineurals are synapomorphous for teleosts. However, epineural processes are present on the anterior vertebrae of *Griphognathus* where they appear to ossify independently (Rosen *et al.* 1981: fig. 54A). Furthermore in *Neoceratodus* the cartilaginous transverse process serves as a boss for the articulation of a cranial rib. Thus the dipnoan transverse process seems more likely to be homologous with an epineural process than with the actinopterygian cranio-spinal process.

The foramen magnum is somewhat higher than it is broad (fm, Figs 1, 2, 3) and much smaller than the entrance to the notochordal canal. The notochordal canal (not, Figs 1, 2, 26) is ovoid in section, a little broader than high and with its long axis extending through the whole of the otic region and terminating in the top of the ventral otic fissure (Figs 16, 20, 26). The width of the notochordal canal diminishes rapidly in an anterior direction (Fig. 26) but then remains the same width up to the fissure. There is no real occipital condyle and the notochordal canal is not lined with a cone of perichordal tissue as in pholidophorids, leptolepids and Recent teleosts (Patterson 1975: 318).

Beneath the notochordal canal lies the aortic canal (cao, Figs 1, 2, 14, 15, 16, 25, 26, 50) which is almost circular in section. The aortic canal leads forwards and downwards to open on the ventral surface on a level with the vestibular fontanelles. The walls of the canal are smooth, perichondrally lined and formed by the basioccipital. The aortic canal narrows somewhat anteriorly, then finally widens into a half-funnel shaped opening with two well-marked grooves diverging from the lateral margins of its mouth. These grooves (gla, Fig. 14) mark the paths of the lateral aortae. Just anterior to the point of bifurcation of the aorta (in BMNH P.53259) there is a small longitudinal crest which marks the point of attachment of the aortic ligament (alig, Figs 14, 50). In other specimens of *Mimia* and in *Moythomasia* this crest is replaced by a small protuberance (Gardiner 1973: fig. 2; sup) in the same position or occasionally placed more anteriorly, that is more distant from the point of bifurcation. The dorsal aorta bifurcated level with the anterior end of the vestibular fontanelle.

In one specimen of *Mimia* (BMNH P.53259, Fig. 15) the aortic canal itself bifurcates anteriorly, as in *Polypterus*, and here the aortic ligament must have originated on the pillar which divides the canal. In this specimen the point of bifurcation lies behind the level of the vestibular fontanelle. In *Kansasiella* (Poplin 1974: fig. 14) the aortic canal is much longer than in *Mimia*; it bifurcates anteriorly (as in P.53259), but additionally has a paired opening in the floor of the canal for the exit of the second efferent arteries. The aortic canal is also very long in *Boreosomus* (Nielsen 1942: fig. 63) but here both the anterior opening and the opening in the floor of the canal (for the second efferents) are unpaired. In *Pteronisculus* (Nielsen 1942: fig. 6) and *Kentuckia* (Rayner 1951: fig. 4) the canal is long, the anterior opening bifurcated, but the opening in the floor single. *Cosmoptychius* (Schaeffer 1971: fig. 8) has a long canal bifurcated anteriorly with no apparent ventral opening.

In pholidopleurids such as *Australosomus* the aortic canal is much shorter, but there is still a well-marked median peg-like process for the attachment of the aortic ligament (Nielsen 1949: figs 5, 6). A similar process (alig, Fig. 7 and see p. 201) can be seen in *Moythomasia* although the aortic canal is much longer.

The wall of the aortic canal is perforated by a large dorsolaterally-directed canal which transmitted the occipital artery (foca, Figs 1, 2, 13, 14, 15). In most specimens there is a single foramen on either side, but in some (BMNH P.53250 for example) there is a single opening for the occipital artery on one side and a double opening on the other, while in other specimens the canal is double on both sides (foca, Figs 4, 5). Allis (1922: 207) described a blind canal in the basi-exoccipital of *Polypterus* in the position of the occipital artery in *Amia* and *Mimia*, but he also showed how the succeeding two intervertebral arteries in *Polypterus* arise as a single artery from the dorsal aorta, then branch into two, the anterior branch passing up (presumably) in relation to the intermuscular septum and the more posterior passing into the cranial cavity through the occipital nerve foramen.

Elsewhere within palaeoniscids and pholidopleurids there is always a dorsolaterally-directed canal for the occipital artery, single in *Pteronisculus* (Nielsen 1942: fig. 9), *Kansasiella* (Poplin 1974: fig. 20) and *Australosomus* (Nielsen 1949: fig. 4) but double in *Kentuckia* (Rayner 1951: figs 4, 7). Although there are two openings on either side for the occipital arteries in *Parasemionotus* (Lehman 1952: fig. 3), in the majority of more advanced actinopterygians the occipital artery, where it occurs, issues through a single opening on either side of the aortic canal or groove (*Lepidotes* Patterson 1975: fig. 109; *Dapedium* Patterson 1975: fig. 113; *Amia* Allis 1897: 706; *Pachycormus* Patterson 1975: fig. 106; pholidophorids Patterson 1975: 320).

At the anterior end of the basioccipital, a small paired perichondrally-lined canal passes anteroventrally down through the bone from a point in the floor of the neurocranium (VI_2, Fig. 25) at the level of the anterior end of the zygal plate (see below, p. 194) to open ventrally in the floor of the orbit dorsolateral to the ventral otic fissure (Figs 16, 20). As it passes into the floor of the orbit this canal enters the ventral edge of the prootic (this can be inferred from BMNH P.53245 in which the perichondral margin of the prootic just encloses the anterior limit of the canal). This canal must have transmitted the abducens nerve (VI, Fig. 29). In one specimen (BMNH P.53234, Fig. 25) the canal is forked dorsally within the basioccipital and each branch is continuous with a short canal in the zygal plate. The cranial entrance to these canals is a pair of oval foramina on the medial surface of each zygal (a similar pair of foramina is also present in

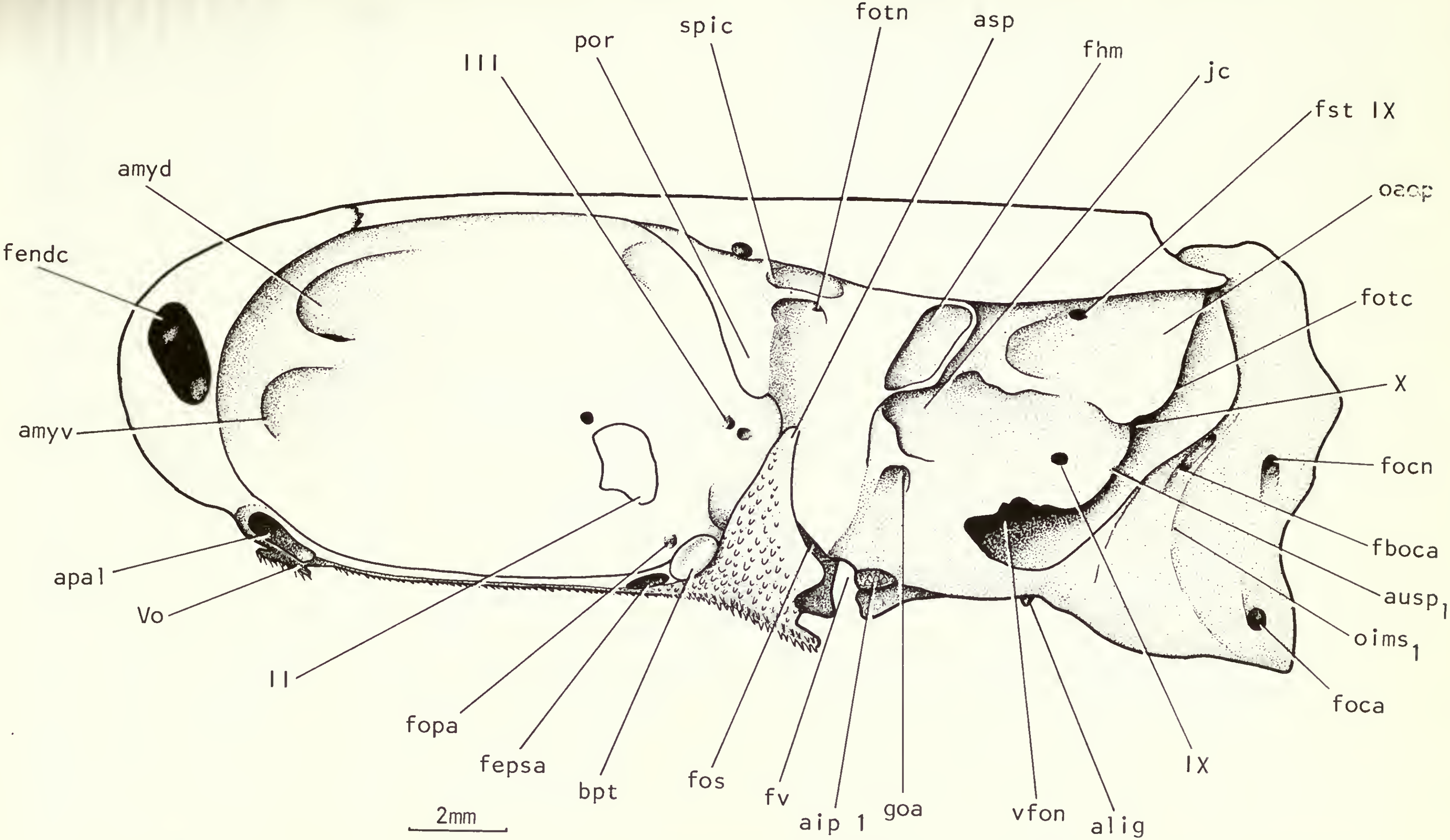
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Fig. 7 *Moythomasia durgaringa* Gardiner & Bartram. Neurocranium in left lateral view. Composite, based on several specimens.

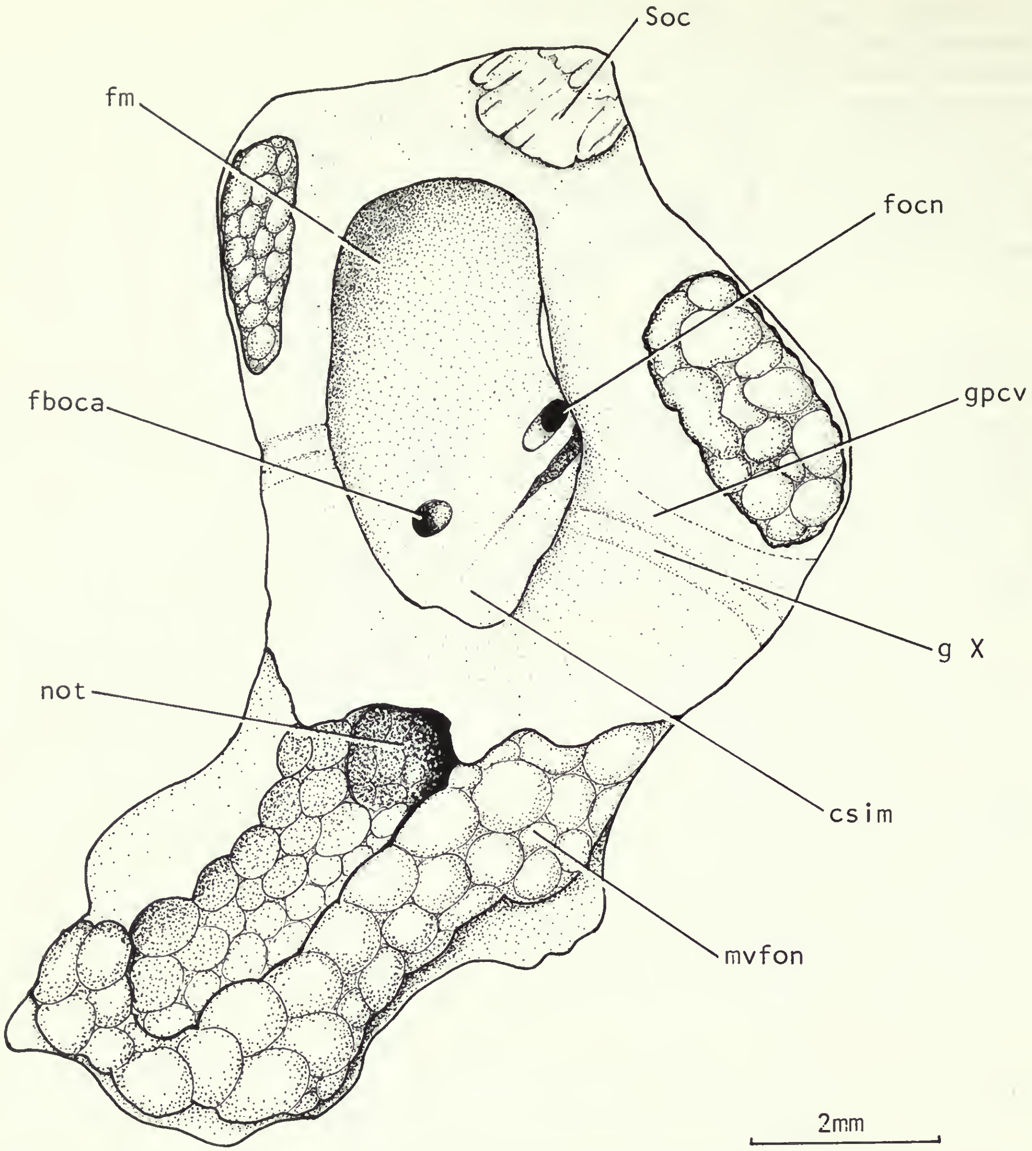


Fig. 8 *Moythomasia durgaringa* Gardiner & Bartram. Occipital region in anterodorsal view, looking into the rear of the vestibular fontanelle from the left side, from BMNH P.53221.

BMNH P.53249). In all living actinopterygians the root of the abducens nerve is double, but in this particular specimen (BMNH P.53234) of *Mimia* the two roots remained separate until they entered the basioccipital. In all other specimens examined the canal for the abducens nerve opens below the zygal plate. However, when there is a single short canal in the posterior region of the zygal, it is always in direct line with the internal opening of the abducens canal. Rayner (1951: fig. 10) suggested that a similar foramen in the zygal plate of Watson's palaeoniscid A served to transmit the abducens nerve. In *Polypterus* (Allis 1922: 228) the canal for the abducens opens in the floor of the cranial cavity immediately posterior to the base of the cartilaginous prootic bridge and runs anteriorly in the cartilage between the basi-exoccipital and basisphenoid, to open by a notch in the edge of the basisphenoid immediately below the trigeminal foramen. Thus the relationship of the abducens is similar in *Mimia* and *Polypterus* except that in the latter the prootic ossification is absent. In other palaeoniscids and pholidopleurids the abducens nerve never passes through the basioccipital. Instead it always leaves the cranial cavity in front of the ventral otic fissure, usually through the prootic bridge (*Pteronisculus* Nielsen 1942: figs 9, 10; *Kentuckia* Rayner 1951: fig. 8, *Kansasiella* Poplin 1974: fig. 23; *Australosomus* Nielsen 1949: fig. 7). In halecostomes such as *Amia*, pholidophorids and most Recent teleosts the abducens nerve passes through the prootic bridge (formed by the prootics into the roof of the myodome. Primitively in actinopterygians the abducens nerve is deduced to have passed through the basioccipital for part of its course, but with rearward migration of the ventral otic fissure this relationship was lost.

The zygal plates arise from the anterior ends of the walls of the notochordal canal and are more or less contiguous with the underlying basioccipital. They rise upwards and outwards at an angle of perhaps 70° and are occasionally joined in the mid-line ventrally by a thin strut of endochondral bone (in the roof of the notochordal canal). In BMNH P.53249, in which much of the internal, perichondral margin of the prootic has not yet fused with adjacent bones (Pro, Fig. 25), the separate nature of the paired zygals can be recognized. They are delicate ossifications completely covered in perichondral bone except along their ventral margins where they are partially fused to be basioccipital. Sometimes there is a small posterior foramen in each zygal, occasionally two foramina, one anterior and one posterior (VI_1, VI_2, Fig. 25; see also Fig. 26). These foramina transmitted the abducens nerve from the floor of the brain into the adjacent canal in the basioccipital. Dorsally each zygal has a distinct notch in its margin; this presumably served for the passage of the auditory nerve from the brain to the otic capsule. That these plates really are separate ossifications can be inferred from the limits of their perichondral covering and from the nature of their endochondral core, which is made up of very small units quite

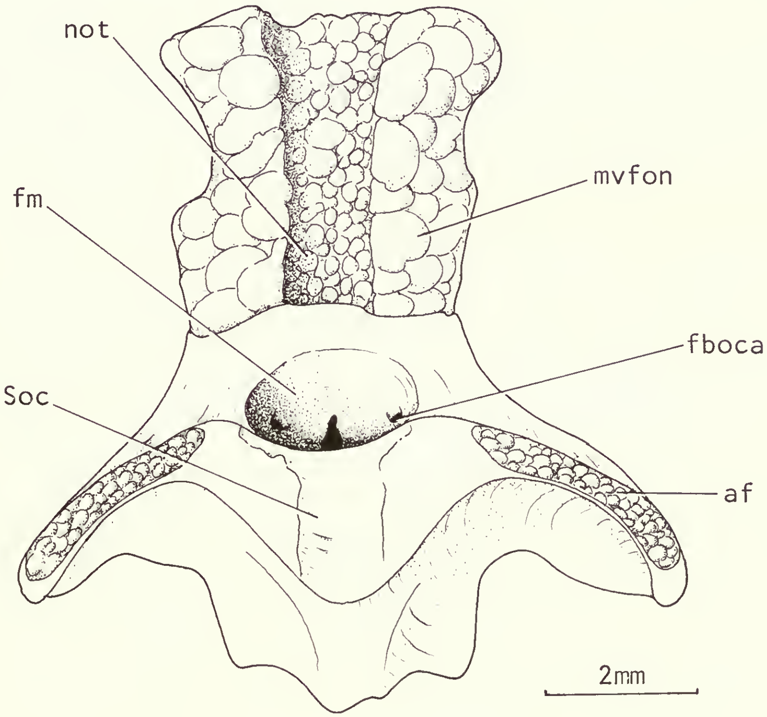


Fig. 9 *Moythomasia durgaringa* Gardiner & Bartram. Occipital region in antero-dorsolateral view, looking into the floor and rear of the vestibular fontanelle from BMNH P.53227.

dissimilar from the large 'bubbles' of bone making up the underlying basioccipital. These plates form the inner wall of the pocket that housed the sacculus, separating it from the floor of the brain. In *Polypterus* a cartilage in a similar position performs the same function. The relationships of these plates to the sacculus can best be seen in a reconstruction of an endocranial cast of *Kansasiella* (Poplin 1974: fig. 23). Zygal plates have previously been recorded in only one other actinopterygian, *Pteronisculus* (Nielsen 1942: fig. 9, om; Bjerring 1971: fig. 6), but they are also recognizable in *Kentuckia* (Rayner 1951: 70 – median projection) and *Kansasiella* (Poplin 1974: fig. 20, t).

In *Pteronisculus* (Nielsen 1942: 53) the displaced zygal plate is obviously a separate ossification since it has no connection with any other bone. Presumably it formed above the notochord and occupied a similar position in life to that in *Mimia*. It is a small, horizontal, bilaterally symmetrical plate, devoid of perichondral lining ventrally. In both *Kentuckia* and *Kansasiella* the zygal plate is shown as a median ossification in the roof of the notochordal canal and is inseparable from the underlying basioccipital, but produced dorsolaterally into perichondrally-lined wings, very similar to the paired zygal plates in *Mimia*. From these four examples it is not possible to decide whether paired or unpaired zygals represent the more primitive condition, but certainly the presence of zygals is primitive (see p. 207) both for actinopterygians and osteichthyans.

Externally the surface of the occipital region around the notochordal canal and foramen magnum is marked by two distinct parallel ridges which run vertically up the lateral walls of the neurocranium. The more posterior ridge starts on the aortic canal just behind the foramen for the occipital artery and runs in a more or less uninterrupted line to fade out dorsally on a level with the middle of the foramen magnum, posterodorsal to the foramen for the occipital nerve. This ridge marks the origin of the second intermuscular septum ($oims_2$, Figs 1, 2, 3, 4). The more anterior of the two ridges also commences on the aortic canal. It is considerably more elevated than the posterior ridge and continues further dorsally and finally peters out well above the foramen magnum. The first intermuscular septum presumably originated ($oims_1$, Figs 1, 2, 3, 4) on this ridge.

In those specimens with only one opening for the occipital artery (BMNH P.53243, Fig. 2) a groove leads anterodorsally from that foramen towards the foramen for the occipital nerve. A little below the occipital nerve foramen the groove bifurcates and the anterior branch proceeds almost horizontally through a gap in the ridge for the first intermuscular septum to pass

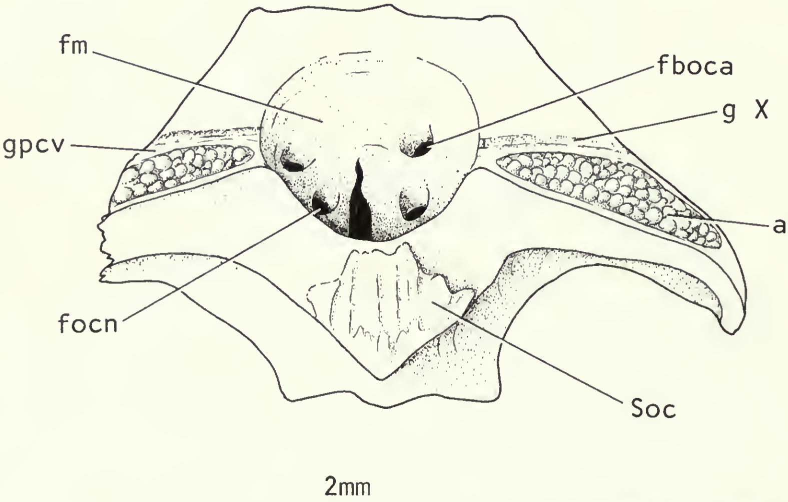


Fig. 10 *Moythomasia durgaringa* Gardiner & Bartram. Dorsal part of the occipital ossification in anterodorsal view, from BMNH P.53221.

immediately into the mouth of a small foramen (fboca, Fig. 2) which gives direct access to the floor of the cranial cavity, anterior to the occipital nerve (see *Moythomasia*, fboca, Figs 8, 9, 10). This short canal runs longitudinally through the bone, and clearly transmitted a blood vessel rather than a nerve. From the disposition of the groove leading to it, the canal must have carried a branch of the occipital artery into the rear of the cranial cavity. The other branch of the groove passes up and turns anterodorsally just below the occipital nerve foramen, passes through a more dorsal notch in the ridge for the first intermuscular septum (gboca, Figs 2, 3), and continues as a groove onto the dorsal surface of the occiput. In one specimen (BMNH P.56496), and on one side only, this dorsal branch passes through a distinct foramen in the ridge (fboca, Fig. 3) for the first intermuscular septum. This dorsal branch must have supplied blood from the occipital artery to the first trunk muscle.

Where there is a double opening for the occipital artery the more anterior opening always lies in front of the ridge for the first intermuscular septum (BMNH P.56501 and P.53234, Figs 4, 5). In these specimens a gutter runs directly from this anterior opening to the entrance of the canal which passes into the cranial cavity (fboca, Figs 4, 5). There can be no doubt here that the canal which opens into the cranial cavity transmitted a branch of the occipital artery. Moreover in these specimens, as the canal for the branch of the occipital artery passes horizontally through the wall of the neurocranium, it gives off another branch dorsally. This branch emerges on the lateral wall on a level with the foramen for the occipital nerve and from its mouth an even more distinct gutter (gboca, Figs 4, 6) runs up onto the dorsal occipital surface. This foramen and gutter carried a branch of the occipital artery to the first trunk muscle, and presumably is equivalent to the dorsal branch of the occipital artery in those forms where the occipital artery is single.

In the inner wall of the foramen magnum there are two foramina, the more anterior of which transmitted the branch of the occipital artery. The more posterior foramen is the larger and the canal from it runs posterolaterally to open just in front of the ridge for the second intermuscular septum. This canal transmitted an occipital nerve (focn, Figs 1, 2, 3, 4, 5, 6, 13). In the floor of the foramen magnum, level with the foramen for the branch of the occipital artery, is a shallow paired depression (see *Moythomasia*, csim, Fig. 8) but whether or not this can be regarded as an incipient cavum sinus imparis depends on interpretation. A more obvious median depression is seen in the palaeoniscid *Pteronisculus* (Nielsen 1942: fig. 5), but the true extent of the cavum sinus imparis is perhaps only seen in teleosts (Patterson 1975: 316). If, however, a vascular plexus did exist primitively in the floor of the foramen magnum then a direct arterial supply would have been an advantage.

Remnants of this rather elaborate occipital arterial blood supply can be recognized in several later forms. Patterson (1975: 292) has described in *Pholidophorus* a dorsolaterally-directed canal which originates in the cranial cavity immediately in front of the occipital nerve and opens on the dorsolateral surface of the exoccipital. This canal anastomoses (within the bone) with an anteriorly-directed canal which opens in the upper part of the vagus canal. Patterson (*ibid.*) suggested that the anterior branches carried a tributary of the posterior cerebral vein while the dorsolaterally-directed canal carried both a vein and a branch of the occipital nerve. There seems little doubt that the dorsolaterally-directed canal is homologous with a similar canal in *Mimia* which, as shown above, served for a branch of the occipital artery. On the other hand in *Pteronisculus* (Nielsen 1942: 38, fig. 5) there is a canal running from the foramen magnum to the hind wall of the vagus canal. This appears to be homologous with the anteriorly-directed canal in *Pholidophorus*. Further, Nielsen (1942: 35) described a possible connection between this canal and a more ventral canal which opens on the occipital surface near the occipital artery (Nielsen 1942: fig. 4, k). In one specimen of *Mimia* (BMNH P.53245) there is, on one side only, a similar connection within the bone between an anteriorly-directed canal which opens in the upper part of the vagus canal and the canal carrying a branch of the occipital artery into the cranial cavity. Thus it is likely that the anteriorly-directed canal in *Pteronisculus* and *Pholidophorus* transmitted yet another branch of the occipital artery. Bjerring's (1971: fig. 6) suggestion that this canal in *Pteronisculus* transmitted a hypothetical branch of the abducens nerve which innervated the subcranial muscle is without foundation (see also Patterson 1975: 294).

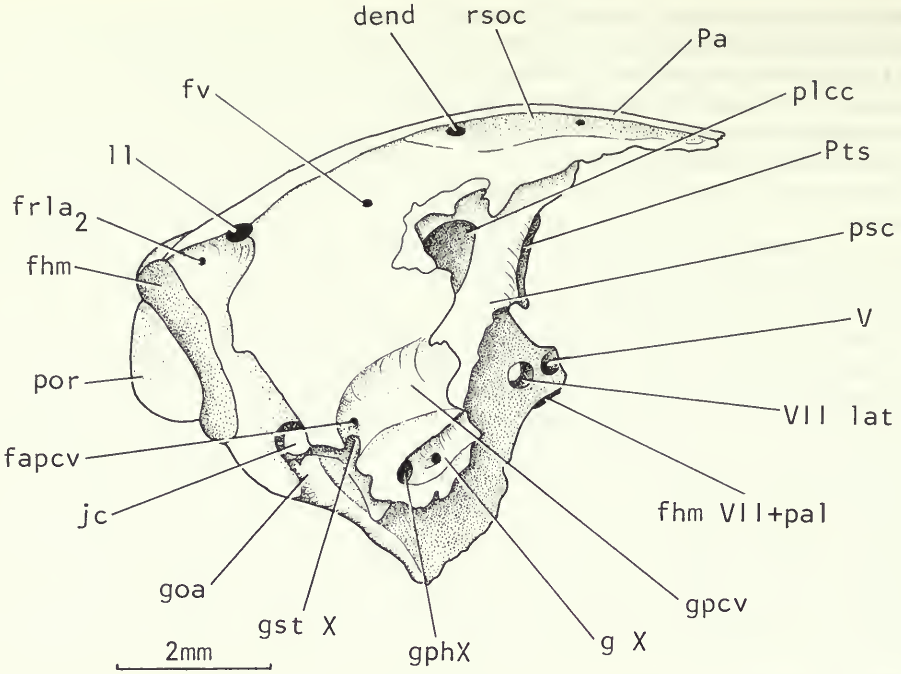


Fig. 11 *Mimia toombsi* Gardiner & Bartram. Left half of otic region of the neurocranium and attached dermal bones in posterior view, from BMNH P.53245.

A dorsolaterally-directed canal originating in the floor of the foramen magnum and opening on the occipital roof is also present in parasemionotids (Patterson 1975: fig. 97), *Caturus* (Patterson 1975: 319), *'Aspidorhynchus'* (Patterson 1975: fig. 100) and *Heterolepidotus* (Patterson 1975: fig. 104). Presumably in all these cases it carried a branch of the occipital artery.

Apart from *Mimia* (and perhaps *Pteronisculus*) the only other palaeoniscid in which a branch of the occipital artery passes directly into the cranial cavity is *Kansasiella* (Poplin 1974: fig. 19, spi).

A single occipital nerve canal as seen in *Mimia* is characteristic of most palaeoniscids (*Pteronisculus, Boreosomus, Kentuckia, Kansasiella*), *Australosomus*, parasemionotids, pholidophorids and leptolepids (Patterson 1975: 319) and is considered to be the primitive condition for actinopterygians. Although this single occipital nerve corresponds to the first occipital nerve of *Polypterus, Acipenser, Polyodon, Lepisosteus* and *Amia*, all these forms have incorporated one or more neural arches and corresponding spino-occipital nerves into the braincase. Similar incorporations are deduced to have occurred in *Birgeria, Saurichthys, Lepidotes* and *Dapedium* (Patterson 1975: 319).

No real evidence for the position of intermuscular septa has previously been produced in palaeoniscids. In fact the only previous record of septal position in fossil actinopterygians is from pholidophorids. On the epioccipital of *Pholidophorus germanicus* (Patterson 1975: 297) a posteriorly-projecting shelf of membrane bone marks the point of origin of the first intermuscular septum, while just behind the external opening of the occipital nerve canal a large trifid projection marks the origin of the second intermuscular septum, much as in *Amia* (Allis 1897) and *Scomber* (Allis 1903). These projections in *Pholidophorus, Amia* and *Scomber* are homologous with the more complete ridges in *Mimia*.

The dorsal face of the occiput above the foramen magnum slopes gently upwards in the mid-line, then at the level of the external opening of the occipital nerve canal it rises steeply to a short median crest. The ridge so formed is not as pronounced as the so-called crista occipitalis of

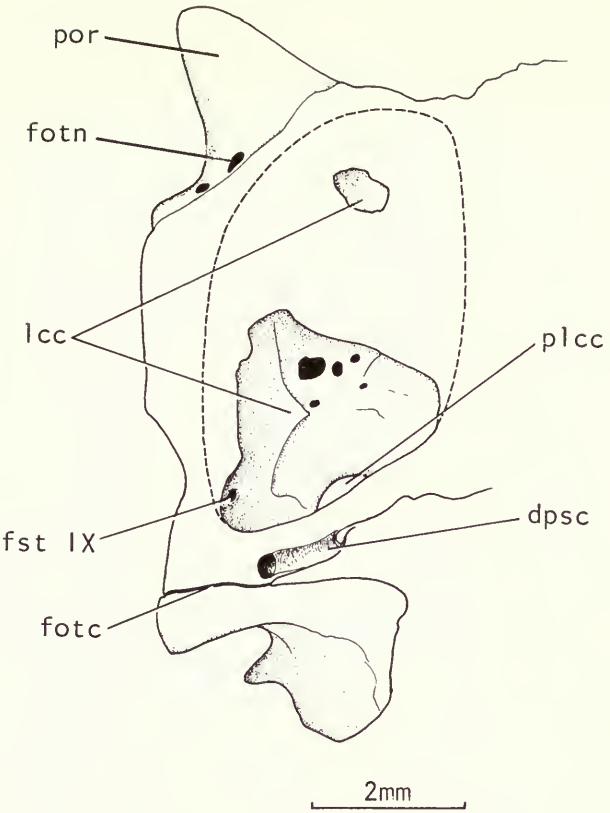


Fig. 12 *Mimia toombsi* Gardiner & Bartram. Left otic and occipital regions of the neurocranium in dorsal view, from BMNH P.53234. The broken line marks the limits of the lateral cranial canal.

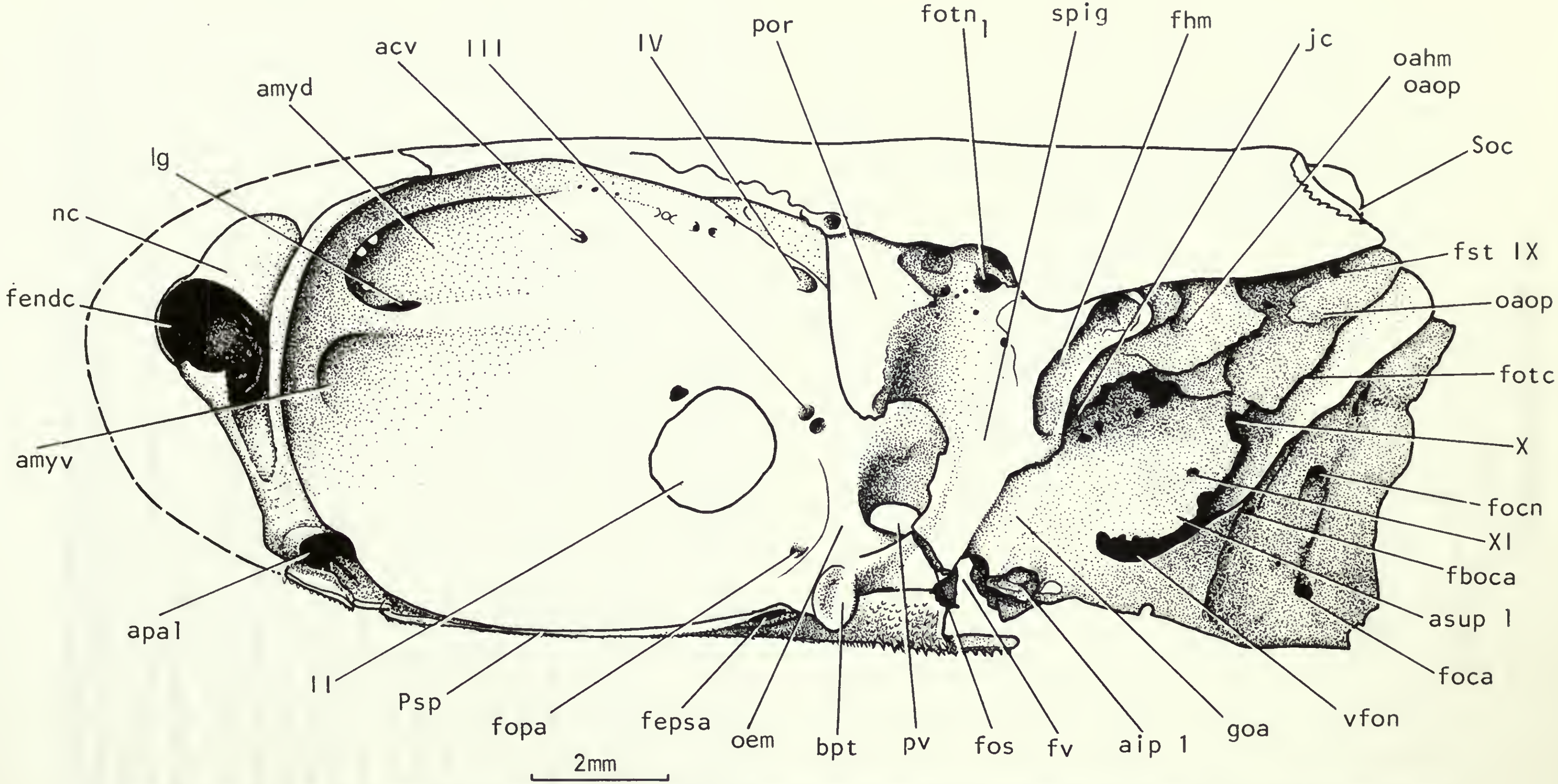
Pteronisculus (Nielsen 1942: fig. 3) or *Kansasiella* (Poplin 1974: fig. 13). Dorsally, just below the supraoccipital, the crest gives way to a triangular prominence which presumably served for the insertion of the longitudinal intervertebral ligament (ivl, Figs 1, 2, 3). In one specimen (BMNH P.53245) the triangular prominence is missing and instead there is a prominent median ridge. Elsewhere in fossil actinopterygians, a distinct cartilage-lined pit in the exoccipital region above the foramen magnum is seen in parasemionotids (Patterson 1975: fig. 98) and in *Dapedium* (Patterson 1975: fig. 113); this marks the insertion of the longitudinal ligament in those fishes. On either side of the median crest in *Mimia* two distinct depressions mark areas of origin of the anterior trunk muscle (oatm, Figs 1, 2, 3).

The canal for the vagus and the nervus lineae lateralis is represented by an inflated part of the occipital fissure. The internal opening of the canal lies some distance above the floor of the foramen magnum from whence it passes posterolaterally to exit immediately posteriorly to the parampullary process. The posterior wall of the vagus canal is divided by a narrow ridge into two roughly equal divisions. The upper division contained the posterior cerebral vein (gpcv, Fig. 11) and the lower the vagus nerve (g.X, Fig. 11), as in *Saurichthys* (Stensiö 1925: fig. 4), *Pteronisculus* (Nielsen 1942: 39) and *Pholidophorus* (Patterson 1975: 293).

Moythomasia durgaringa

The occipital region in this species is very similar to that of *Mimia* and only the salient differences will be noted.

The posterior dorsal fontanelle is perichondrally lined and larger than in *Mimia* (Gardiner 1973: fig. 7). The occipital fissure is more steeply inclined and the vestibular fontanelle much



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focn
XI
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apal
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fopa
fepsa
oem
bpt
pv
fos
fv
aip 1
goa
vfon
2mm

Fig. 13 *Mimia toombsi* Gardiner & Bartram. Neurocranium in lateral view, from BMNH P.56498 (partly after Gardiner & Bartram 1977).

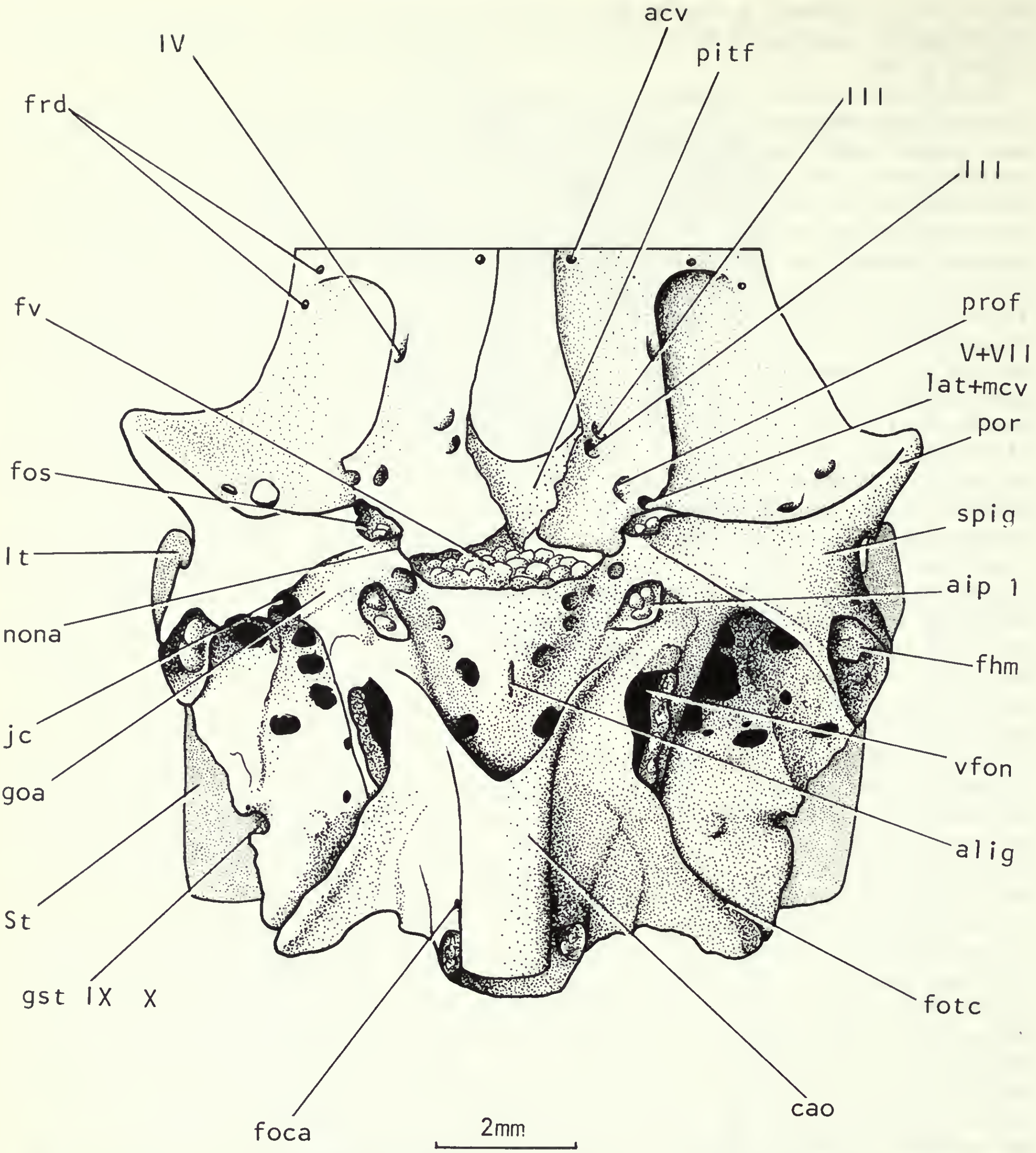
larger than in *Mimia*, nearer in size to that of *Pteronisculus*. The occipital fissure is perichondrally lined except for a large oval area between the vagus canal and supraoccipital (Figs 8, 9, 10).

The ventral otic fissure occupies a similar position to that in *Mimia* although it is not quite as extensive dorsomedially (fv, Fig. 29). The occipital region occupies less than 17% of the total neurocranial length (measured through the vagus foramen) and, unlike *Mimia*, is higher than any other portion. A more clearly definable centre of ossification, presumably representing the supraoccipital, can be recognized in some specimens (BMNH P.53221) but the cranio-spinal process is a little more ventral than in *Mimia*, level with the bottom of the foramen magnum. The foramen magnum is marginally wider than high while notches in the hind ventral wall of the notochordal canal similar to those in *Mimia* show ossification to be incomplete in these areas. The aortic canal is similar in shape and size to that of *Mimia* but the peg-like process for the attachment of the aortic ligament (alig, Fig. 7) is much more prominent and more posterior in position, lying immediately in front of the anterior opening of the aortic canal. The wall of the aortic canal is perforated by a single, dorsolaterally-directed canal for the occipital artery, but even though the ridge for the insertion of the second intermuscular septum is not as distinct as in *Mimia*, the course of the occipital artery is clear. A groove leads up from the foramen for the occipital artery (BMNH P.53221) towards the foramen for the occipital nerve, and just below this latter foramen the groove branches. One branch passes anteriorly, leads through a gap in the ridge for the first intermuscular septum, and immediately enters a small foramen from which a canal runs horizontally inwards to open in the anterior floor of the foramen magnum (fboca, Figs 8, 9, 10). As in *Mimia*, this canal must have transmitted a branch of the occipital artery into the floor of the cranial cavity. The other branch of the groove passes anterodorsally through a more dorsal gap in the ridge for the first intermuscular septum, then up towards the top of the occiput. Each of these paired grooves terminates in a foramen on either side of the mid-line, below the insertion of the intervertebral ligament. Each foramen connects, by means of a short anteroventrally-directed canal, with the cranial cavity above the foramen magnum. In one specimen (BMNH P.51380, Gardiner 1973: fig. 7) the two grooves terminate in a single foramen, set just off centre, below the insertion of the intervertebral ligament. These dorsal grooves and foramina transmitted a second branch of the occipital artery into the dorsal half of the cranial cavity. The only other osteichthyans in which similar dorsal openings have been described are the Devonian dipnoans *Griphognathus* and *Chirodipterus* (Miles 1977: figs 12, 16, nut) but in these forms the canals end blindly in the cranial bone.

In the floor of the foramen magnum, anterior to the opening for the branch of the occipital artery, there is a shallow paired depression which possibly housed the cavum sinus imparis. Normally, the floor of the foramen magnum posterior to this depression is unossified in the mid-line (Fig. 8) but in one specimen (BMNH P.56502) the floor is complete and raised in a distinct median ridge which runs from the depression to the hind margin of the foramen magnum. In some specimens a small foramen in the groove for the posterior cerebral vein (BMNH P.56502) could have transmitted another branch of the occipital artery. Dorsally, below the supraoccipital, a well-marked triangular area with several small protuberances must have served for the insertion of the intervertebral ligament.

Occipital region: discussion

1. *Posterior dorsal fontanelle.* A distinct posterior dorsal fontanelle seems to be confined within actinopterygians to the palaeoniscids and chondrosteans such as *Acipenser* (Bridge 1878), although Patterson (1975: 307) has suggested that an imperfectly ossified area in front of the supraoccipital in *Pholidophorus bechei* represents the remains of a small, paired posterior dorsal fontanelle. Elsewhere a distinct posterior dorsal fontanelle is seen in the rhipidistian *Eusthenopteron* (Jarvik 1954: figs 21B, C), where it appears as a crescent-shaped opening in the roof of the supraotic cavity, and in *Acanthodes* (Miles 1973*a*: fig. 3), where it is similar in shape and size to that in *Mimia*. Whether this is a true dorsal fontanelle in *Acanthodes* or merely a cartilaginous area devoid of perichondral ossification could not be determined. Miles (1977: 101) has convincingly homologized the posterior dorsal fontanelle of *Eusthenopteron* with openings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aip 1
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jc
vfon
goa
alig
St
gst IX X
fotc
cao
foca
2mm

Fig. 14 *Mimia toombsi* Gardiner & Bartram. Occipital, otic and orbitotemporal regions of neurocranium and attached dermal bones in ventral view, from BMNH P.53259. Parasphenoid and basisphenoid missing.

of the paired endolymphatic ducts in the dipnoans *Griphognathus* and *Chirodipterus*, which differ from Recent dipnoans in having an external opening for the endolymphatic duct on the dermal skull roof. It is possible that in gnathostomes the posterior dorsal fontanelle primitively served for the exit of the endolymphatic ducts to the surface of the chondrocranium, since in xenacanth sharks (Schaeffer 1981: 22) the unpaired, slit-shaped endolymphatic fossa is confluent with the occipital fissure, and in *Moythomasia* the paired endolymphatic ducts open into the dorsal fontanelle.

2. *Occipital fissure.* Apart from palaeoniscids a completely uninterrupted, perichondrally-lined occipital fissure is only known in the pholidopleurid *Australosomus* (Nielsen 1949, Beltan 1968) and in the teleost *Pholidophorus* (Patterson 1975: 417). However, in the latter there is no obvious posterior dorsal fontanelle and parts of the fissure may be covered superficially by membranous outgrowths from the intercalar and supraoccipital. In *Perleidus* cf. *stoschiensis* (Patterson 1975: 460) the fissure is still perichondrally lined from the vagus canal up to the medial margin of the epioccipital and pterotic.

Not surprisingly perhaps, remnants of this perichondrally-lined fissure can be seen in several other actinopterygian groups. Within the amioids and in some parasemionotids (Patterson 1975: 434) the perichondral lining persists from the vagus canal to just above the external semicircular canal, while in some pachycormids (Patterson 1975: 448) a small area opposite the medial part of the intercalar is perichondrally lined. In the earliest known leptolepid braincase, from the Sinemurian, the perichondrally-lined portion of the cranial fissure still extends from the vagus canal up to the lower margin of the epioccipital.

Patterson (1975: 418) has shown how the occipital fissure is closed in pholidophorids, leptolepids and several other groups of actinopterygians by three distinct processes: obliteration of parts of the fissure by cartilage (this requires simple ontogenetic fusion of the occipital arch with the otic capsule prior to ossification), obliteration by forward extension of the occipital bones into the otic region, or the development of membrane bone outgrowths to bridge the fissure. In living chondrosteans the occipital fissure is obliterated by cartilage in *Acipenser*, and in *Polypterus* its path is represented by the suture between opisthotic and basi-exoccipital (Patterson 1975: 463).

From this brief survey of the occipital fissure in actinopterygians it is evident that a perichondrally-lined fissure is primitive (Gardiner 1973: 106; Patterson 1975: 567). Apart from actinopterygians an occipital fissure is found in acanthodians (*Acanthodes*, Miles 1973*a*: 66), Palaeozoic selachians (*Xenacanthus, Tamiobatis*, Schaeffer 1981), where it is presumed to have been cartilage-filled and uncalcified, early dipnoans (Miles 1977), and rhipidistians (Jarvik 1954: fig. 1; 1972: 64). In all described actinistians the occipital fissure is obliterated, and as in *Polypterus* represented by sutures between bones. In *Laugia* membranous outgrowths from the occipital region further obliterate it (Forey, personal communication).

I have argued elsewhere (Gardiner 1973: 129) that a perichondrally-lined occipital fissure is primitive for osteichthyans (see also Patterson 1975: 466) and is a synapomorphy they share with acanthodians. More detailed examination, however, has convinced me that in *Acanthodes bronni* the fissure is not perichondrally lined.

3. *Vestibular fontanelle.* This lies at the anteroventral corner of the occipital fissure, usually anterior or ventral to the glossopharyngeal foramen, and is open in all known palaeoniscid braincases; it is large in *Pteronisculus* (Nielsen 1942: 48) and *Kentuckia* (Rayner 1951: fig. 7). Though the fontanelle was cartilage-filled in *Mimia* (see particularly Figs 14, 15, 25) the upper part at least is perichondrally lined in *Pteronisculus* (Nielsen 1942: 48), and in *Boreosomus* (Nielsen 1942: 290) the whole fontanelle is perichondrally lined. Apart from these two palaeoniscids no other actinopterygian has been described in which the vestibular fontanelle has a perichondral lining. A vestibular fontanelle is still seen in the pholidopleurid *Australosomus* (Nielsen 1949: 41) and in *Perleidus* (Patterson 1975: 460), but in the latter it is often obliterated in more fully ossified skulls. Within the amioids a large fontanelle persists in some parasemionotids (Patterson 1975: 434), whereas in others such as *Ospia* and some individuals of *Watsonulus* it is again obliterated. A quite large fontanelle persists in pachycormids (Patterson 1975: fig. 106) while in the primitive teleost *Pholidophorus bechei* (Patterson 1975: fig. 56) the fontanelle is as large as in *Mimia*. In some other species of *Pholidophorus* the fontanelle is closed. In Recent teleosts the vestibular fontanelle can often be recognized in the adult neurocranium as an area of membrane or cartilage at the junction of the prootic, basioccipital and exoccipital. Thus it would seem that primitively in actinopterygians the vestibular fontanelle was cartilage-lined and confluent with the cranial fissure.

The vestibular fontanelle clearly corresponds to the basicapsular fenestra of the embryo

(Patterson 1975: 466). In the embryo the basicapsular fenestra is that space between the auditory capsule and the parachordal cartilage, bounded anteriorly by the embryonic connection of the capsule to the parachordals, the anterior basicapsular commissure (de Beer 1937: 399). A long metotic fissure separates the otic capsule from the parachordals posteriorly in both selachians and osteichthyans, and the basicapsular fenestra is eventually closed off posteriorly by the posterior basicapsular commissure, but this often happens quite late in ontogeny: not until the 9·5 mm stage in *Amia* (Pehrson 1922) or the 11 mm stage in *Lepisosteus* (Veit 1911, Hammarberg 1937). Thus, in the palaeoniscids and other primitive actinopterygians, the relationship of the vestibular fontanelle to the occipital fissure resembles that seen in early fish embryos.

A vestibular fontanelle, cartilage-filled in life, is also present in the rhipidistians *Eusthenopteron* (Jarvik 1954: fig. 1) and *Youngolepis* (Chang 1982: fig. 10), and an area of the braincase wall of *Acanthodes* (Miles 1971*a*: fig. 4.7, Jarvik 1977: fig. 3) anteroventral to the occipital fissure and devoid of perichondral bone possibly included the vestibular fontanelle. Miles (1977: 49) has argued that since the fontanelle is filled with cartilage in most primitive actinopterygians, and can thus close in bone during ontogeny, it is devoid of phylogenetic significance. Hence, though dipnoans lack a fontanelle they do not differ significantly from primitive actinopterygians and *Eusthenopteron* in this respect. However, from the history and occurrence of the vestibular fontanelle I regard the absence of the fontanelle in dipnoans as a derived character, in contrast to its absence in palaeoniscids and *Eusthenopteron*.

The vestibular fontanelle is obliterated in actinistians but persists in tetrapods where it forms the fenestra ovalis of the auditory capsule. A vestibular fontanelle has also been recorded in fossil selachians (*Xenacanthus, Tamiobatis,* Schaeffer 1981: figs 5, 21).

From the arguments outlined above for the occipital fissure and from the fact that the vestibular fontanelle is present in selachians, actinopterygians, rhipidistians and tetrapods I conclude that a cartilage-lined fontanelle is a primitive gnathostome character.

4. *Ventral otic fissure.* In the Gogo palaeoniscids *Kansasiella, Pteronisculus macropterus* and *Boreosomus*, the ventral otic fissure is separate from the vestibular fontanelle.

In other palaeoniscids such as *Pteronisculus stensioei* (Nielsen 1942: figs 4, 6), *Kentuckia* (Rayner 1951: fig. 9) and *'Ambipoda'* (Beltan 1968: fig. 4) the ventral otic fissure passes through the base of the otic region and runs into the vestibular fontanelle; thus the endocranium contains two median ossifications in the adult. However, since the position of the ventral otic fissure in the Gogo palaeoniscids represents the gap between the trabeculae (+polar cartilages) and parachordals in the embryo (Gardiner 1973: 106) and is in an identical position to the ventral part of the intracranial joint in rhipidistians (*Eusthenopteron* Jarvik 1954; *Glyptolepis* Jarvik 1972) and actinistians (*Latimeria* Millot & Anthony 1958, 1965; *Diplocercides* Bjerring 1972: fig. 3), the anterior position of the fissure must be primitive for osteichthyans (Gardiner 1973: 107). Subsequently in actinopterygian evolution the fissure migrated backwards, as the myodome developed, and became confluent with the vestibular fontanelle and the occipital fissure (Gardiner 1970, 1973: 106; Patterson 1975: 541; Gardiner & Bartram 1977: fig. 8). Bjerring (1978) however, has denied the homology of the intracranial joint with the ventral otic fissure, and Schaeffer & Dalquest (1978) have doubted the migration of the ventral otic fissure in actinopterygians.

In all other actinopterygians, where it is possible to distinguish the two fissures, the ventral otic fissure is a ventral continuation of the occipital fissure, through the vestibular fontanelle. In *Polypterus* the ventral otic fissure persists as a broad tract of cartilage between basisphenoid (= sphenoid) and basioccipital, but in *Australosomus* (Nielsen 1949: fig. 4) it is much narrower and clearly opens into the vestibular fontanelle. Similarly in lightly ossified specimens of *Perleidus* (Patterson 1975: 460) and in *Birgeria* the ventral otic fissure is represented by a large tract of cartilage contiguous with the vestibular fontanelle.

In *Amia* and *Lepisosteus* the fissure is represented by a broad band of cartilage between the basioccipital and prootics. In parasemionotids (Patterson 1975: 434), though often obliterated externally, the ventral otic fissure is visible as a suture on the internal bone surface. The fissure is also observable in *Lepidotes* (Patterson 1975: 450), young individuals of pachycormids, later pholidophorids and leptolepids (Patterson 1975: 466). In all living teleosts it is represented by the suture or cartilage between the prootics and basioccipital. From the position of the ventral otic fissure in *Mimia* (and perhaps *Polypterus*, see above) it appears that primitively the fissure passed between the basioccipital and basisphenoid (ossifications deduced from Patterson 1975) at least in its most ventral part (Gardiner & Bartram 1977: 230). Subsequently, as a consequence of myodome formation and accompanying rearward migration of the fissure, the prootics replace the basisphenoid as the anterior margin of the ventral otic fissure in later actinopterygians.

Patterson (1975: 466) has shown that in many primitive actinopterygians, such as *Saurichthys*, some specimens of *Perleidus* and parasemionotids, early caturids, *Dapedium*, and early pholidophorids and leptolepids, all forms in which sutures do not persist in the fully ossified braincase, the ventral otic fissure may close completely. This is of interest in relation to the possibility of neurokinesis in actinopterygians. Schaeffer (1968: 216) has argued that where confluence of the ventral otic fissure and occipital fissure has occurred there is the possibility of the two halves of the neurocranium moving relative to one another and that a flexible joint existed in palaeoniscids. I have argued elsewhere (Gardiner 1970: 286) that in primitive palaeoniscids, at least, there was never any neurokinesis, whereas Patterson (1975: 418) has demonstrated that no such kinesis could have occurred in philodophorids. Patterson (1975, and see above) has also shown how, within almost every actinopterygian group, closure of one part or another of the two fissures has taken place. It would appear that the only possible candidates for neurokinesis are those post-Devonian palaeoniscids such as *Pteronisculus* (Nielsen 1942), *Kentuckia* (Rayner 1951), *Paramblypterus* (Heyler 1969), *'Ambipoda'* (Beltan 1968) and the pholidopleurid *Australosomus* (Nielsen 1949) in which the ventral otic fissure and occipital fissure are continuous and the parasphenoid ends at the ventral otic fissure. But in *Pteronisculus* there are species (*P. macropterus*) in which the two fissures are still separate (Beltan 1968: pl. 2), while in *Australosomus* the configuration of the dermal skull roof (Nielsen 1949: fig. 21) makes neurokinesis highly unlikely. Furthermore, no living cladistian or chondrostean shows any semblance of neurokinesis. Therefore it is highly unlikely that any actinopterygian ever exhibited neurokinesis (see also Pearson & Westoll 1979: 386).

As stated earlier (p. 204) it is my belief that the ventral otic fissure corresponds to the ventral part of the intracranial joint in actinistians and rhipidistians (Gardiner 1970: 286; Gardiner 1973: 108). Jarvik (1954, 1960, 1968, 1972) and Bjerring (1967, 1973) have insisted that the intracranial joint is a persisting vertebral joint and therefore primitive for gnathostomes. This has led to some disagreement over the exact position of the ventral otic fissure in actinistians and rhipidistians. Jarvik (1954) believed that the more posterior position of the ventral fissure in *Pteronisculus* was primitive and homologized it with a cartilage-filled fissure in an apparently similar position, linking the vestibular fontanelles in *Eusthenopteron*. Bjerring (1971) on the other hand claimed that it was homologous with his 'anterior intraotic joint' and later (Bjerring 1973) insisted that the intracranial joint was not homologous in rhipidistians and actinistians. These arguments have been critically reviewed at length elsewhere (Miles 1975, 1977; Patterson 1975; Gardiner & Bartram 1977; Wiley 1979) and as Miles (1977: 50) succinctly summed them up, 'the best reason for rejecting Jarvik's and Bjerring's conclusions is that they lead to unacceptable phylogenetic results.' No such difficulties arise if we consider a ventral otic fissure as primitive for osteichthyans and the intracranial joint a shared specialization of actinistians and some rhipidistians (see also Rosen *et al.* 1981: 259).

Finally, the condition of the ventral otic fissure in dipnoans is of interest since it closely parallels that of later actinopterygians (Miles 1977: 50). Although there is no myodome in dipnoans, the ventral otic fissure has migrated posteriorly and is covered by a long parasphenoid stem. In the Gogo dipnoans *Griphognathus* and *Chirodipterus* (Miles 1977: figs 13, 17) the ventral otic fissure is already continuous with the occipital fissure, there is no expanded vestibular fontanelle and the median portion of the ventral otic fissure has been obliterated externally, much as in some parasemionotids. I have suggested elsewhere (Gardiner 1973: 108) that early phylogenetic obliteration of this inherent line of weakness in the braincase floor of dipnoans is related to their specialized feeding habits and to the concomitant fusion of the palatoquadrate and neurocranium. The parasphenoid also grew back to close over the the ventral otic fissure in later actinopterygians and possibly in tetrapods other than ichthyostegids (but see Rosen *et al.* 1981: 259).

5. *Supraoccipital.* This does not occur in *Polypterus* or *Acipenser* or in any fossil or living lepisosteoid, amioid, pachycormid or semionotid (Patterson 1975: 432–450); nevertheless it is characteristic of pholidophorids and teleosts. However, since a supraoccipital may be present in palaeoniscids such as *Mimia* and *Moythomasia*, its absence in amioids, pachycormids and semionotids could be a derived condition. A supraoccipital occurs in actinistians and tetrapods, and the median ossification in the upper margin of the occipital arch of *Eusthenopteron* (Jarvik 1975: fig. 9), immediately behind the posterior dorsal fontanelle, may also represent a supraoccipital.

The presence of a supraoccipital is therefore considered a primitive osteichthyan condition.

6. *Aortic canal.* This is always present in palaeoniscids and is a common feature in other primitive actinopterygians. Patterson (1975: 320) has demonstrated how the point at which the dorsal aorta bifurcated and the aortic ligament originated on the braincase migrated backwards in actinopterygian evolution; he suggested this movement may be correlated with enlargement of the circulus cephalicus (or lengthening of the lateral aortae). This rearward migration of the point of bifurcation of the dorsal aorta presumably resulted in shortening or obliteration of the aortic canal. In other forms where the lateral aortae remain short, such as *Acipenser, Polyodon* (Danforth 1912: 442, fig. 15), *Amia* and *Lepisosteus* (Goodrich 1930), backward growth of the parasphenoid may also have caused loss of the aortic canal (Gardiner 1973: 116). A short but distinct canal still exists in some parasemionotids (*Broughia* Stensiö 1932*b*: 270), the semionotid *Dapedium* (Frost 1913: fig. 1; Gardiner 1960: fig. 38, and in some leptolepids (Patterson 1975: 319). In Recent teleosts an aortic canal has been reported in the notopterid *Xenomystus* (Taverne 1973) but Patterson & Rosen (1977: 129) have shown this to be a neomorph produced in relation to the ear/swimbladder connection. An aortic canal is clearly a primitive feature in actinopterygians.

There is no aortic canal in actinistians, and the canal is also absent in dipnoans and rhipidistians. That the canal should be missing in dipnoans and rhipidistians is not surprising since in both groups there is good evidence to show that the dorsal aorta bifurcated behind the occiput (*Ectosteorhachis* Romer 1937: fig. 1; *Eusthenopteron* Jarvik 1954: fig. 7; *Chirodipterus* Säve-Söderbergh 1952, Miles 1977: fig. 18; *Neoceratodus* Sewertzoff 1902: 593). Miles (1977: 56) has suggested that absence of the aortic canal in dipnoans is secondary and correlated with backward expansion of the parasphenoid, but it seems more likely to be related to the fact that dipnoans, like primitive tetrapods, have long lateral dorsal aortae (or epibranchial arteries) and this places the point of bifurcation of the aorta behind the occiput. Moreover, expansion of the parasphenoid has not occurred in actinistians or rhipidistians, yet they all lack an aortic canal. Despite there being no aortic canal in dipnoans and no sign of an aortic ligament in Recent dipnoans, Miles (1977: fig. 13) considered a pit on the hind face of the occiput in *Griphognathus*, between the parasphenoid and cranial centrum, to be the site of origin of the aortic ligament. He (1977: 56) further suggested that a similar notch in the back of the parasphenoid in *Birgeria* (Nielsen 1949: fig. 62) was for the aortic ligament. In actinopterygians where there is any evidence of an aortic ligament, even in Recent clupeoids, salmonoids and cyprinoids, the point of attachment is always to the basioccipital and not, as in *Griphognathus*, to the base of the cranial centrum. Moreover, it is difficult to believe that *Birgeria* differs from all other described palaeoniscids, *Polypterus* and chondrosteans in having the bifurcation of the dorsal aorta behind the occiput, particularly since a similar notch in the back of the parasphenoid is to be seen in *Polypterus, Saurichthys* (Stensiö 1925) and *Chondrosteus* (RSM 1887.15.2).

Outside osteichthyans an aortic ligament is said to have been present in *Acanthodes* (Miles 1973*a*: fig. 5), but the only record of an aortic canal other than in actinopterygians is in the holocephalan *Helodus* (Moy-Thomas 1936: fig. 4). In all living selachians the paired lateral aortae are comparatively shorter than in *Polypterus, Acipenser, Amia* and *Lepisosteus*, and the dorsal aorta bifurcates behind or just at the level of the occiput. The lateral aortae are often enclosed in paired canals in primitive selachians such as *Cladodus* (Gross 1937: fig. 5), *Cladoselache* (Harris 1938: 9), *Tamiobatis* (Romer 1964) and xenacanths (Schaeffer 1981: fig. 6); they are similarly enclosed in the living carcharhinoid *Dirrhizodon* (Compagno 1973: 19). In other fossil selachians such as *Hybodus* (Maisey 1983) the lateral aortae lay in well-marked grooves beneath the occipital region much as in *Megalichthys*. In placoderms such as *Wijdeaspis* (Young 1978) there are long paired grooves on the occipital region which must have housed the lateral aortae, but in *Brindabellaspis* (Young 1980: fig. 7) the lateral aortae pass through separate canals as in *Cladodus*.

A median aortic canal is therefore present only in actinopterygians and holocephalans, and it is not possible to decide whether it has arisen independently in the two groups or is a primitive gnathostome character.

7. *Canal for abducens nerve*. Primitively in actinopterygians the abducens nerve passed through the basioccipital and entered the orbit through the corner of the prootic. In *Latimeria* (Millot & Anthony 1958) the abducens is said to pass down through the floor of the saccular cavity without piercing any ossification. This course is not surprising since the basioccipital is small and confined to the posterior end of the neurocranium. However, in the rhipidistian *Eusthenopteron* Jarvik (1972: fig. 93) has restored the neurocranium with a foramen for the abducens in the edge of the ossification lateral to the notochord. This foramen is in the prootic (deduced from a similar ossification in actinopterygians and *Latimeria*), but in *Eusthenopteron*, as in *Latimeria*, the basioccipital does not extend ventrally beneath the anterior portion of the notochord. The path of the abducens in dipnoans is difficult to follow; for example, in the development of *Neoceratodus* the abducens is intimately connected with the roots of the facial and trigeminal nerves (Fox 1965: 505). Nevertheless this nerve never passes through the prootic bridge as in later actinopterygians; in the Devonian *Chirodipterus* (Miles 1977: figs 17, 21) it is presumed to pass laterally with V and VII through the prootic area. In the development of amphibians such as *Ambystoma* (Goodrich 1911) the abducens nerve still pierces the anterior parachordal (so called because the parachordal is restricted to the extreme anterior end of the notochord) to emerge on the ventral surface of the skull.

I conclude that in osteichthyans the abducens nerve primitively passed through the basioccipital.

8. *Zygal plates*. In primitive actinopterygians such as *Mimia* paired zygal plates are found in the roof of the notochordal canal. Similar plates are also present in *Moythomasia*, but in other palaeoniscids such as *Pteronisculus* the zygal plate is median and unpaired. In actinopterygians zygal plates are found only in palaeoniscids. They appear to be present in all actinistians. In *Nesides* (Bjerring 1971: 194) the zygals are said to be paired, but in *Latimeria* (Millot & Anthony 1958: pl. 17) there is a median, bilobed plate. In rhipidistians paired zygals have been reported in *Eusthenopteron* (Bjerring 1971: 192) but in *Glyptolepis* (Jarvik 1972: 68) there is a median plate as in *Latimeria*.

From this distribution we may conclude that paired zygal plates are a primitive osteichthyan feature. It is easy to see how, with increase in size of the myodome and concomitant regression of the notochordal canal, they have been lost in later actinopterygians. The zygals appear to play an important part in the intracranial joint in *Latimeria* and some rhipidistians; they are missing in dipnoans and tetrapods.

9. *Occipital artery*. Primitively, this appears to be related to the second permanent myomere, since in both *Mimia* and *Moythomasia* the foramen for the artery arises between the ridges for the insertion of the first and second intermuscular septa. This direct relationship, also seen in *Amia*, is recognizable in any other actinopterygian, but in the rhipidistian *Ectosteorhachis* (Romer 1937: fig. 2) the foramen for the occipital artery opens in the line of the ridge for the second intermuscular septum and presumably belongs to the second permanent segment, not

the third as suggested by Romer (1937: 8). Support for this view can be obtained from one specimen of *Mimia* (BMNH P.54501) in which that part of the basioccipital around the aortic canal and notochord projects posteriorly for some distance as it does in *Ectosteorachis*. Furthermore, in the development of *Polypterus* Allis (1922: 208) has demonstrated how the basioccipital portion of the basi-exoccipital can project posteriorly beyond its exoccipital portion to a distance equal to about half that of the first free vertebra and still be part of the segment anterior to it (that incorporating the ventral root of the second occipital nerve). Elsewhere an occipital artery has been described in *Eusthenopteron* where it is also presumably related to the second permanent occipital segment (Jarvik 1975: fig. 8). A similar dorsolaterally-directed canal has also been described in Devonian dipnoans (Säve-Söderbergh 1952: figs 1, 8; Miles 1977: figs 11, 15, 23), but its relationships with neighbouring foramina is not clear. The course of the occipital artery has been described in *Neoceratodus* (Spencer 1893: 10) and an artery in a similar position exists in urodeles (Drüner 1901) and anurans (Gaupp 1899). In placoderms such as *Brindabellaspis* (Young 1980: fig. 7) the occipital artery passed into the cranial cavity in the vicinity of the first occipital nerve, and then appears to have run backwards through the occiput. Finally in *Acanthodes* (Miles 1973*a*: fig. 3) the foramen for the occipital artery again appears to be related to the second occipital segment since it lies in front of the opening for the second occipital nerve (first occipital, see below).

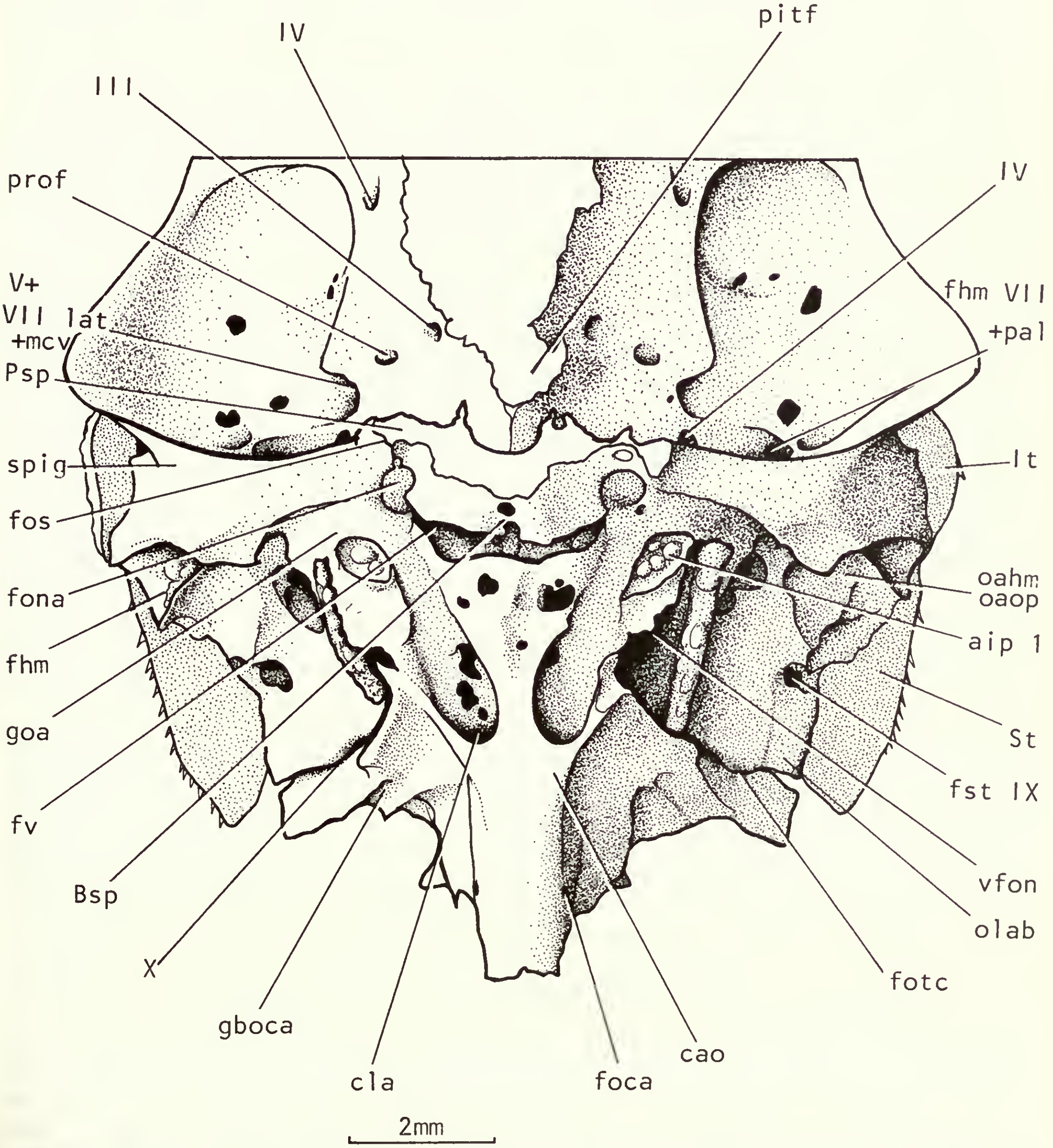
The primitive course of the occipital artery after leaving its canal in the basioccipital is less certain. In *Amia* (Allis 1897: 706) it runs up over the lateral surface of the basioccipital and exoccipital onto the dorsal surface of the occiput, where it sends branches to all occipital myomeres. In *Polypterus*, although there is no occipital artery as such, the first intervertebral artery apparently takes over its function. In a 75 mm larva, Allis (1922: 207) has shown how the intervertebral artery divides into two and the anterior branch passes into a canal in the basioccipital. From thence one part of it passes into the cranial cavity through the second occipital nerve canal and the other continues up towards the second intermuscular septum. The posterior branch also enters the cranial cavity, but through the canal for the ventral root of the first spinal nerve. Unfortunately, in other living osteichthyans the occipital artery either does not groove the surface or does not enter the occiput, consequently there is no model on which to base the distribution of the various branches. Nevertheless, a system of grooves for the branches of this artery has been recognized in the rhipidistian *Eusthenopteron* (Bjerring 1971: fig. 18; Jarvik 1975: fig. 9).

From the evidence given above for both *Mimia* and *Moythomasia* the canal which enters the anterior floor of the foramen magnum after running through the exoccipital at right angles to the long axis of the neurocranium must have carried a branch of the occipital artery and not an occipital nerve. If this is so then the canal in a corresponding position in *Kansasiella* (Poplin 1974: figs 24, 25) must also have served for a branch of the occipital artery. It follows that a canal with identical relationships and running at right angles to the long axis of the brain in the rhipidistian *Ectosteorhachis* (Romer 1937: fig. 9) must also have served for a branch of the occipital artery, not the first occipital nerve as suggested by Romer (1937: 8). It should be noted that occipital nerves normally run obliquely backwards to their points of exit. It also seems likely that in *Acanthodes* (Miles 1973*a*: fig. 2) the foramen lying in the groove for the occipital artery transmitted a branch of that artery rather than the first occipital nerve.

10. *Segmental structure of occiput.* In view of the variable composition of the occipital region in Recent fishes and the loss of somites from the metotic series during development, determination of the primitive number of adult occipital myomeres is difficult. For example, among actinopterygians *Polypterus* has incorporated one centrum into its braincase, *Amia* two, *Lepisosteus* three, and *Acipenser* up to eight; among dipnoans *Neoceratodus* has added three.

In the Gogo palaeoniscids there must have been at least two permanent myomeres, more probably three, judged from the position of the two intermuscular septa and the single occipital nerve canal. A similar condition existed in pholidophorids and leptolepids (Patterson 1975: 318). In all these forms the first myomere is characterized by the absence of any canal for an occipital nerve. From this evidence I conclude that the ancestral condition for actinopterygians is a single occipital nerve canal (which carried a ventral root only) related to the second permanent myomere.

In *Latimeria* (Millot & Anthony 1958) both the basioccipital and the paired exoccipitals are much reduced; nevertheless, together with the 'supraoccipital' these ossifications must represent the first and only occipital sclerotomes, since they are associated with the first trunk muscle. There is no corresponding occipital nerve; instead the associated nerve leaves the foramen magnum posterior to this segment. Other Recent bony fishes in which the first occipital myomere has either no related ventral nerve root, or if it does, whose nerve exists in a more


IV
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fotc
gboca
cao
cla
foca
2mm

Fig. 15 *Mimia toombsi* Gardiner & Bartram. Occipital, otic and orbitotemporal regions of neurocranium and attached dermal bones in ventral view, from BMNH P.56483. Anterior regions of parasphenoid and basisphenoid missing.

posterior segment, include *Amia* (Allis 1897: 725), *Polypterus* (Allis 1922: 207), *Lepisosteus* (Schreiner 1902), and *Lepidosiren* (Bridge 1898). Furthermore, in the development of the amphibian *Ambystoma* (Goodrich 1911) the first permanent myomere never has a ventral root. On the other hand *Cryptobranchus* (de Beer 1927) is said to be unique among living amphibians in possessing one pair of occipital foramina, but there is evidence of two segments in this animal.

In *Ectosteorhachis* (Romer 1937), *Rhizodopsis, Eusthenopteron* (Jarvik 1975) and *Youngolepis* (Chang 1982) there is evidence from the imprint of the intermuscular septa and the course of the occipital artery of three occipital myomeres, as in *Mimia*. Two pairs of foramina have also been described in the occiput of all four genera. The posterior pair (posterior spino-occipital nerve canals of Jarvik 1975) corresponds to the occipital nerve (ventral root) foramina of *Mimia*, while the anterior pair (anterior spino-occipital nerve canals of Jarvik 1975) occupies a similar position to foramina I attribute to branches of the occipital artery in *Moythomasia* and *Mimia*.

In *Griphognathus* and *Chirodipterus* (Miles 1977) the occipital foramen is followed posteriorly by three pairs of spino-occipital nerve foramina, and in *Holodipterus, Dipterus* and *Conchopoma* (Schultze 1975) by at least two pairs of spino-occipital nerve foramina. The skull of *Neoceratodus* (Fox 1965) includes three occipital arches (one occipital and two spino-occipital), that of *Protopterus* (de Beer 1937) two, and *Lepidosiren* one (Agar 1906). In *Protopterus* the occiput is pierced by a single pair of occipital nerves and in *Neoceratodus* the occiput encloses two pairs of spino-occipital nerves.

In many selachians the occipital nerves leave either through the vagus canal or behind the condyles. Nevertheless, in *Scyllium* (de Beer 1937), where the occiput is believed to comprise three segments, the occipital arch is pierced by a single pair of occipital nerves. In *Xenacanthus, Tamiobatis* (Schaeffer 1981) and *Hybodus* (BMNH P.50869) the occipital region is pierced by at least three (four in *Hybodus*) pairs of nerve foramina, but foramina are apparently wanting in *Cladoselache, Cobelodus* and *'Cladodus'* (Schaeffer 1981).

In placoderms there are invariably several pairs of occipital nerve foramina; up to seven pairs of spino-occipital nerves have been described in *Buchanosteus* (Young 1979), five pairs in *Brindabellaspis* and three pairs in *Ctenurella* (Miles & Young 1977).

Finally in *Acanthodes* the basioccipital is almost as extensive as in *Mimia* and incorporates the foramen for the occipital artery, whereas the 'lateral occipital' includes the foramen for the occipital nerve as well as a more anterior foramen (Miles 1973*a*: fig. 2, on1) for a branch of the occipital artery.

From this brief survey I conclude that the first myomere of osteichthyans is characterized by the absence of an occipital nerve.

11. *Longitudinal intervertebral ligament.* The presence of this is a primitive feature for gnathostomes (Goodrich 1930: 21), and in later actinopterygians such as parasemionotids and semionotids the ligament terminated in a deep, cartilage-lined pit in the exoccipital region above the foramen magnum. A comparable pit in the same region has been described in the Devonian dipnoans *Griphognathus* and *Chirodipterus* (Miles 1977: figs 12, 16), and an unossified area immediately above the foramen magnum in *Eusthenopteron* (Jarvik 1975: fig. 10) presumably served the same function.

Otic and orbitotemporal regions

Review of ossification centres

The otic and orbitotemporal regions of the braincase consist of a single ossification which shows few sutures, apart from the otico-sphenoid fissure. Several of the more lightly ossified specimens of *Mimia* (BMNH P.56495, P.56496) and *Moythomasia* (BMNH P.56480) do, however, show partial gaps in the perichondral lining of the internal surface of the neurocranium, which give some indication of the internal extent of the individual ossifications. The external extent of these ossifications is occasionally marked by faint sutures and by the more obvious fissures (ventral otic fissure, otico-sphenoid fissure; fv, fos, Fig. 22). From such specimens it is possible (by comparison with *Perleidus*, parasemionotids and pholidophorids) to estimate the extent of the individual bones with confidence. Thus in *Mimia* and *Moythomasia* it appears that the prootic ossifies around a centre in the lateral commissure and occupies only a small part of the outer lateral wall of the braincase and the posteroventral corner of the orbit, but probably includes the trigeminal and facial foramina. Internally the prootic forms the anterolateral wall of the otolith chamber and the ampullary chambers of the anterior and external semicircular canals. Dorsally the prootic forms the the anteromedial portion of the lateral cranial canal. I conclude that the prootic forms a smaller part of the braincase than in parasemionotids and a considerably smaller part than in pholidophorids (Patterson 1975). This discrepancy may be directly related to the absence of a myodome in the Gogo palaeoniscids, since in pholidophorids, leptolepids and Recent teleosts where the myodome is extensive the prootic is proportionally larger. The prootic is large in fossil actinistians and *Latimeria* (Millot & Anthony 1958) where the bone extends posteroventrally as far as the ventral fissure and posterolaterally to the hyomandibular facet.

The prootic is small in *Acipenser* and occupies only the posteroventral corner of the orbit. In *Polypterus* the prootic is a transient ossification only seen in embryos (Pehrson 1947: 405), where it forms a small perichondral thickening around the posterior margin of the trigeminal foramen. Elsewhere within the palaeoniscids a prootic is absent from *Birgeria* (Nielsen 1949). In all these forms the ascending process of the parasphenoid is long and complex and covers that lateral area of the neurocranium normally occupied by the prootic. A prootic is not obviously present in *Acanthodes* (see for example Miles 1973*a*: fig. 2; Jarvik 1977: fig. 3). The prootic appears to have been a small ossification (smaller than the opisthotic) in primitive actinopterygians. Its increase in size and importance in later halecomorphs and teleosts is presumed to be related to myodome formation, whereas its large size in actinistians may be related to the absence of a sphenotic.

A separate stout sphenotic ossifies from a centre in the postorbital process. In *Mimia* it is presumed to extend posteriorly as far as the hyomandibular facet which marks the junction between it and the opisthotic. A wide groove on the face of the postorbital process housed the spiracle which opened dorsally on the skull roof. An endoskeletal spiracular canal is absent, but occasionally a pair of processes partially delimit the top of the spiracular groove (Fig. 14; Gardiner 1973: fig. 5). Similar processes in *Moythomasia* (Fig. 28) may join to form a complete bar (spic, Figs 7, 30). An endoskeletal spiracular canal is characteristic of most palaeoniscids (*Pteronisculus, Boreosomus, Kentuckia, Kansasiella, Birgeria* etc.), *Perleidus* (Stensiö 1932*b*: fig. 59), *Australosomus* (Nielsen 1949), many fossil halecostomes including *Pholidophorus* (Patterson 1975: 399) and all extant chondrosteans and holosteans; it is absent in *Polypterus*. Within primitive actinopterygians a separate sphenotic has been described in *Cosmoptychius* (Watson 1928; Schaeffer 1971), *Perleidus* (Patterson 1975), *Birgeria* and *Polypterus* and is universally present in halecomorphs and teleosts. A similar ossification of the postorbital process in *Acanthodes* (Miles 1973*a*: fig. 1; Jarvik 1977: fig. 3) may also be a sphenotic since, as in primitive actinopterygians, it forms the anterior margin of the hyomandibular facet; the suggestion by Jarvik (1977: 207) that the head of the hyomandibula articulated with the middle of the otic ossification is considered unlikely since in ossified neurocrania the hyomandibular facet always lies at the junction of two or more ossifications. An ossified postorbital process is also present in placoderms (*Buchanosteus* Young 1980) and a tesserate postorbital process is a prominent feature of most chondrichthyans. The sphenotic is apparently missing from those actinistians in which separate ossifications have been described (*Wimania* Stensiö 1921, 1925; *Macropoma, Whiteia* Beltan 1968: 114; *Rhabdoderma* Forey 1981; *Latimeria* Millot & Anthony 1958) and a single ossification occupies the area of the basisphenoid, pterosphenoid and sphenotic. This ossification also includes the postorbital process (antotic process of other authors). The postorbital process is missing in *Ectosteorhachis* and *Rhizodopsis* whereas in *Eusthenopteron, Holoptychius* and *Glyptolepis* (Jarvik 1972: figs 20, 21) it is represented by the suprapterygoid process.

The anterior internal limits of the opisthotic can be estimated from *Mimia* (BMNH P.56496). Its external limits can be confirmed partly from *Cosmoptychius* (Schaeffer 1971: fig. 8, ot), where a separate opisthotic forms the anterior wall of the vagus canal and includes the canal for the glossopharyngeal nerve and a groove for its supratemporal branch (Watson 1928: 49), and partly from *Polypterus* where the bone is very large.

The opisthotic in *Mimia, Cosmoptychius* (Schaeffer 1971: fig. 8A), *Pteronisculus* (Nielsen 1942: 16; fig. 3) and *Perleidus* (Patterson 1975: fig. 115) has a posteroventral tongue and includes the lower portion of the posterior semicircular canal as well as the external semicircular canal. The centre of ossification in *Mimia* (and *Moythomasia*) is around the ampulla of the posterior semicircular canal and is indicated by the downwardly projecting parampullary process (pamp, Fig. 6) but it extends anteriorly to meet the sphenotic, thereby forming the posterior margin of the hyomandibular facet. The hyomandibular facet also marks the junction between the opisthotic and sphenotic in *Pteronisculus* and *Perleidus*. Anterodorsally the opisthotic provides a large facet for the origin of much of the constrictor hyoideus dorsalis (oahm + oaop, Figs 1, 4, 5, 13) muscle. In the 75 mm *Polypterus* described by Allis (1922: 219) the opisthotic begins to form around the projecting hind end of the otic capsule; that is, around the base of the posterior semicircular canal. In the large specimen of *Polyodon* described by Bridge (1878) the opisthotic is represented by a thin perichondral ossification superficial to the ampulla of the posterior semicircular canal. In *Acipenser* it forms in a comparable position between the foramina of the glossopharyngeal and vagus nerves (Holmgren & Stensiö 1936: fig. 336). The opisthotic is absent in semionotids, *Amia* and *Lepisosteus* as well as leptolepids and more advanced teleosts.

There is a well-marked parampullary process in actinistians (*Nesides*, Bjerring 1977: fig. 23; *Latimeria*, Millot & Anthony 1958) and in several forms (*Macropoma, Laugia, Wimania*, Stensiö 1921) this is borne on a discrete, small ossification which, by comparison with actinopterygians, must be an opisthotic. The probable centre of an opisthotic in rhipidistians is indicated by the postotical process in *Eusthenopteron* (Jarvik 1954: figs 1, 21) and the 'paroccipital process' in *Ectosteorhachis* (Romer 1937: fig. 1). In both cases the centre of ossification is inferred to lie lateral to the base of the posterior semicircular canal. In actinistians the centre of ossification appears to lie somewhat more anteriorly, around an opening in the wall of the labyrinth cavity (Jarvik 1954: fig. 4, fplab) just in front of the parampullary process. The opisthotic seems to be large in early actinistians and rhipidistians. In *Nesides* (Jarvik 1954: fig. 4; Bjerring 1977: fig. 23) and *Rhabdoderma* (Forey 1981: fig. 1) the opisthotic forms most of the lateral wall of the braincase from the vagus foramen to the hyomandibular facet (both dorsal and ventral parts).

The remaining ossification in the otic region is the pterotic. The extent of this can be inferred partly by comparison with *Perleidus*, where the pterotic is quite small and occupies the posterodorsal corner of the otic capsule (Patterson 1975: fig. 115), and partly from the radiating structure of the bone which is recognizable in several specimens. From this evidence the centre of ossification of the pterotic may be estimated as lying within a dorsolateral prominence in the posterior otic region which presumably served for the origin of the posterior part of the constrictor hyoideus dorsalis (oaop, Figs 4, 5, 6, 13). The constrictor hyoideus dorsalis also originates on the upper outer corner of the otic region of the skull in Recent chondrichthyans such as *Heptanchus, Squalus* and *Galeus*. The pterotic is missing in *Birgeria, Polypterus* and *Acipenser*; in *Polypterus* the posterior part of the constrictor hyoideus (the adductor opercularis) originates on the opisthotic. The pterotic is proportionally much larger in *Pholidophorus* than in *Mimia* and forms the greater part of the subtemporal and post-temporal fossae but, as in *Mimia*, the centre of ossification is at the posterolateral shoulder of the otic capsule (Patterson 1975: fig. 75), just posterior to the foramen for the supratemporal branch of the glossopharyngeal nerve. In leptolepids and advanced teleosts the pterotic is much reduced, probably as a result of the closure of the cranial fissure (Patterson 1975: 380), its centre of ossification being located along the external semicircular canal.

In *Amia, Lepisosteus* and *Lepidotes* there is only one bone in the posterodorsal region of the skull; this may be interpreted as either an epioccipital or a pterotic. Patterson (1975: 443) believes that in *Amia* this so-called 'epiotic' probably represents an epioccipital which has extended forwards following the loss of the pterotic. Since the pterotic primitively appears to have served for the origin of the posterior part of the constrictor hyoideus dorsalis and this muscle (adductor opercularis) partly originates on the intercalar in *Amia* it is reasonable to suppose that the remaining ossification is the epioccipital (associated as it is only with trunk

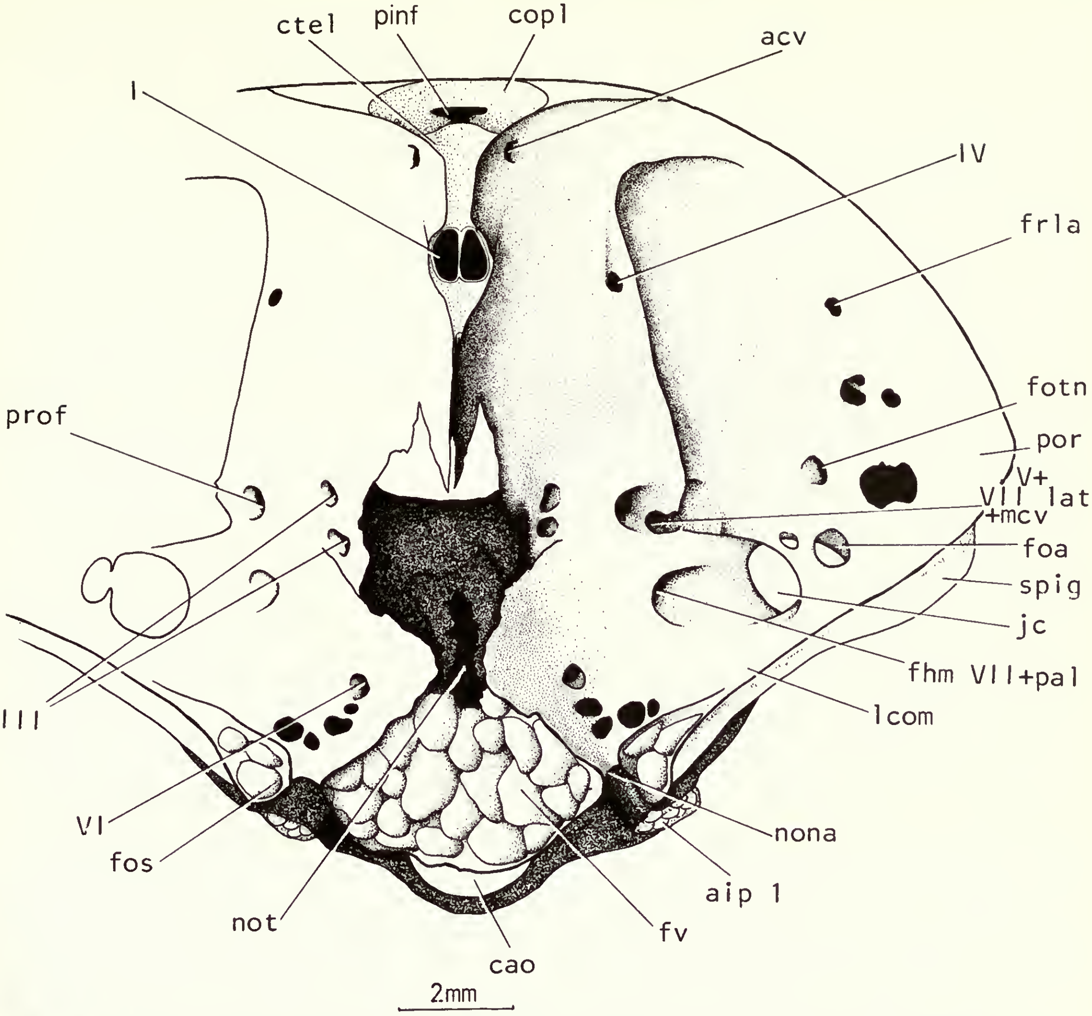

Fig. 16 *Mimia toombsi* Gardiner & Bartram. Otic and orbitotemporal regions of neurocranium in anterior view, as if cut through the middle of the orbit, from BMNH P.53259.

musculature). Patterson (1975: 453) further concluded that in *Lepidotes* this bone represents the pterotic because it includes a blind pit which resembles a dorsolateral expansion of the cranial cavity in the palaeoniscid *Boreosomus* (Nielsen 1942: fig. 66, lv). In *Lepisosteus* it is also likely to be the pterotic since the adductor opercularis is attached to the lateral surface of this bone.

In *Acanthodes* (Miles 1973*a*: fig. 2, swpamp) a distinct boss, on the braincase wall below the jugular canal and the foramen for the glossopharyngeal nerve, housed the posterior ampulla (but see Jarvik 1977: fig. 3 where a similar swelling lies above the jugular canal). The ridge above this ampullary boss delimits the jugular groove and appears to be the centre of ossification of the otic capsule and presumably also served for the origin of the constrictor hyoideus dorsalis. The centre of ossification of the capsule is more dorsal than the opisthotic in *Mimia* and this together with the presumed muscle origin suggests that the ossification is better homologized with the pterotic than with the opisthotic.

The whole orbital region of the Gogo palaeoniscids, apart from the basipterygoid process, is ossified as a perichondral shell penetrated by perichondrally-lined canals for nerves and blood vessels. Presumably there were three pairs of ossifications, basisphenoid, pterosphenoid and orbitosphenoid, as in *Amia* and many teleosts. A separate pterosphenoid has been described in *Pteronisculus* (Nielsen 1942: 90). The basisphenoid is an extensive ossification and its paired nature can be seen in *Mimia* (BMNH P.56483, Fig. 15). Posteriorly it consists of a vertical pillar which flares dorsally into a pair of dorsolaterally-directed arms which join the orbital surface just beneath the oculomotor foramen to form the dorsum sellae (Gardiner & Bartram 1977: 230). Beneath the bridge the junction of the basioccipital with the basisphenoid is marked by the ventral otic fissure. The basisphenoid extends anteriorly for a short distance beneath the orbit to the level of the optic fenestra. The basisphenoid also appears to be paired in *Pteronisculus* (Nielsen 1942: fig. 2) and its centres of ossification are inferred to lie on either side of the vertical pillar, as in *Mimia*. It has been argued elsewhere (Gardiner & Bartram 1977: 237) that the cup-shaped depressions on the basisphenoid pillar in *Mimia* were the points of origin of at least three of the recti muscles. In *Polypterus* (Allis 1922: 252) three of the recti muscles originate (by a short tendinous stalk) on the basisphenoid near its ventral edge and immediately posterior to the optic foramen (as in selachians). The fourth muscle (internal rectus) has its origin slightly more anteriorly, still on the basisphenoid, but anterior to the optic foramen. During development the basisphenoid of *Polypterus* arises from paired perichondral lamellae between the optic and oculomotor foramina. Thus its centre of ossification lies at the point of insertion of the rectus muscles. In other primitive fossil actinopterygians where separate ossifications have been recognized the basisphenoid is only clearly delimited in *Perleidus* (Patterson 1975: 457), and even here it is fused with the prootics.

The basisphenoid in *Pholidophorus bechei* (Patterson 1975: 381) not only forms the pillar but also extends ventrally to form the endochondral floor of the orbit. In later pholidophorids this vental part is less thoroughly ossified while in leptolepids and advanced teleosts all that remains is a slender pedicel consisting mainly of membrane bone. In most halecomorphs the basisphenoid is a median bone forming little more than the pedicel, as in later pholidophorids. In *Amia*, however, the basisphenoid is a small paired ossification which ossifies late in the transverse 'bolster' in front of the floor of the myodome. Thus, the centre of ossification of the basisphenoid is ventrolateral to that in *Mimia, Polypterus* and teleosts. Since three of the rectus muscles originate on this transverse 'bolster' in *Amia* the concomitant shift in ossification centre is hardly surprising. The basisphenoid in pachycormids is not very different from that in *Pholidophorus*, while within the semionotids the basisphenoid of *Lepidotes* is stout and median, and confined to the posteroventral corner of the orbit. In *Lepisosteus* there is no basisphenoid, the rectus muscles originating on the floor of the orbit, lateral to the interorbital septum. Although the shape of the 'basisphenoid' in actinistians suggests that it arises from paired centres, it is never paired either in fossil material or in the embryo (Forey, personal communication). The basisphenoid in *Acanthodes* (Miles 1973*a*: figs 8, 9) is also a large, unpaired ossification, but is similar in size and shape to that seen in *Mimia*. Its centre of ossification is inferred to lie at the base of the basisphenoid pillar.

That a separate pterosphenoid was present in the orbit of *Mimia* can be deduced from the presence of a distinct ridge running upwards from the trigeminal foramen to the roof of the orbit (Figs 16, 17, 20), and from the presence of a pedicel over the trigeminal and facial foramina in *Moythomasia* (Figs 29, 30). The ridge presumably represents the centre of ossification of the pterosphenoid. The limits of the pterosphenoid can be determined with a fair degree of confidence from estimates of distances between neighbouring ossification centres. From this type of analysis the pterosphenoid appears to occupy well over half of the posterior orbital surface. It extends laterally to just beyond the foramen for the otic nerve, where it meets the sphenotic (junction often marked by a series of fenestrae), and ventrally to just above the trigeminal and facial foramina, where it meets the prootic. It extends anteroventrally to just below the oculomotor foramen where it meets the basisphenoid. Together with the orbitosphenoid the pterosphenoid forms a complete interorbital septum (Fig. 13). Thus the pterosphenoid is possibly a large ossification as in other palaeoniscids and contributes to much of the posterior orbital surface.

A small paired pterosphenoid is found in *Acipenser* but it is absent in *Polypterus*. The pterosphenoid is large in halecomorphs ('*Aspidorhynchus*', Patterson 1975: figs 99, 101;

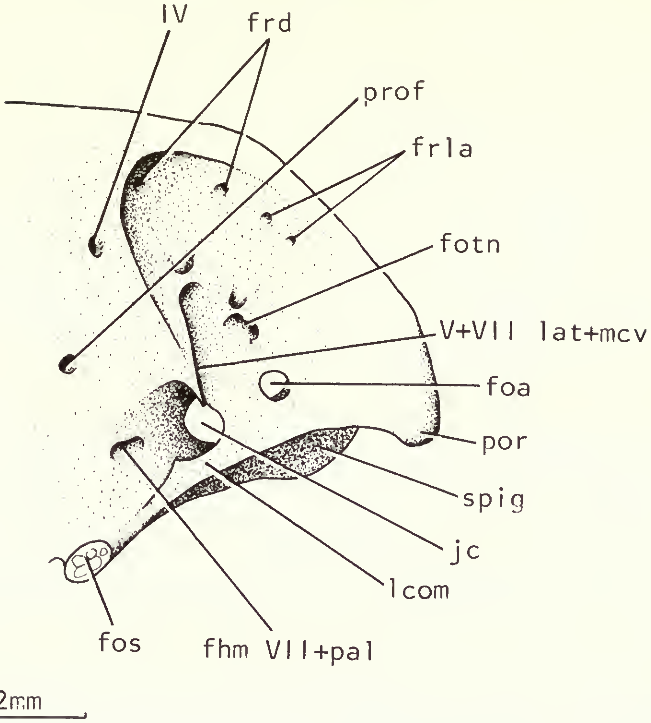

Fig. 17 *Mimia toombsi* Gardiner & Bartram. Left orbitotemporal region of neurocranium in anterior view, from BMNH P.56504.

Macrepistius, Schaeffer 1971: figs 3, 4), semionotids (*Lepidotes*, Patterson 1975: figs 108, 109), pachycormids (*Pachycormus*, Patterson 1975: fig. 106) and pholidophorids (*Pholidophorus*, Patterson 1975: 382). Therefore it seems likely that primitively in actinopterygians the pterosphenoid was an important constituent of the posterodorsal orbital surface. A similar, large dorsal perichondral ossification in the orbit of *Acanthodes* (Miles 1973*a*: fig. 4; Jarvik 1977: fig. 2) may have included an ossification centre homologous with that of actinopterygians.

In actinistians (*Rhabdoderma* Forey 1981: fig. 1; *Latimeria* Millot & Anthony 1958) there is a single ossification centre in front of the prootic. This ossification fills the area occupied by the basisphenoid, pterosphenoid and possibly the sphenotic in actinopterygians, and also bears the postorbital process (= antotic process). The postorbital process is stout and provides an articulation for the dorsal surface of the palate. In *Acanthodes* (Miles 1973*a*: figs 2, 15) and some rhipidistians such as *Eusthenopteron* and *Holoptychius* (Jarvik 1954, 1972) the postorbital ossification also bears an articulatory facet for the palate.

Mimia toombsi

The otic region of the neurocranium is separated from the occipital ossification by the posterior dorsal fontanelle dorsally and the occipital fissure laterally, but ventrally the two regions pass into one another without any distinct boundary. The posterior face of the otic region is lined with perichondral bone from the vestibular fontanelle upwards, thus the subvagal portion of the fissure is open (Fig. 25) as in *Pteronisculus, Kansasiella* and some individuals of *Pholidophorus bechei* (Patterson 1975: 232). The perichondral lining is interrupted at the level of the lateral cranial canal (plcc, Figs 11, 12) but otherwise extends dorsomedially to the posterior dorsal fontanelle. Two notches near the posterior margin of the opening of the cranial cavity lead into a pair of shallow, ventrolaterally-directed grooves. The more dorsal groove is the broader and contained the posterior cerebral vein (gpcv, Fig. 11) and a small foramen within the groove

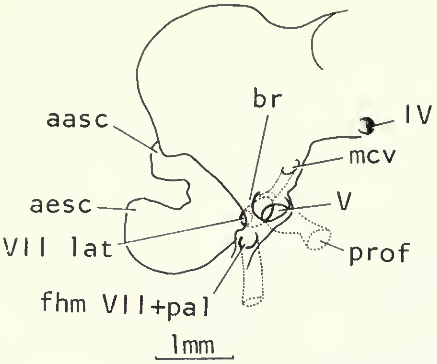

Fig. 18 *Mimia toombsi* Gardiner & Bartram. Internal, medial view of left utricular recess, trigeminal and facial foramina, from BMNH P.56504. Intramural passages indicated by broken lines.

(fapcv, Fig. 11) must have transmitted a small vein into the ampullary cavity of the posterior semicircular canal as in *Pholidophorus bechei* (Patterson 1975: fig. 59). The lower groove was occupied by the vagus nerve, while a large foramen near its lateral limit (gph.X, Fig. 11) which leads out anterolaterally onto the surface of the otic region served for the passage of the pharyngeal branch of the vagus. In other specimens of *Mimia* (cf. BMNH P.56501, Fig. 4) the pharyngeal branch merely notched the end of the vagal canal. A further notch (gst.X, Fig. 11) in the posterolateral margin of the dorsal groove marks the passage of the supratemporal branch of the vagus onto the lateral otic wall.

Below the vagus groove the posterior face of the otic region turns forwards and the perichondral lining gives way to a cartilage-filled vestibular fontanelle (vfon, Fig. 13) as in *Pteronisculus* and other palaeoniscids. The dorsal surface of the otic (Fig. 12) and orbitotemporal regions (Figs 33, 34) is complete and the only opening is the pineal foramen (Pl. 1; pinf, Fig. 33). There is no anterior dorsal fontanelle, in contrast to *Polypterus, Pteronisculus* (Nielsen 1942: fig. 7), *Kansasiella* (Poplin 1974: fig. 12), *Kentuckia* (Rayner 1951: fig. 6) and *Pholidophorus* (Patterson 1975: fig. 60). There is also no fossa bridgei and the recurrent lateralis branch of the facial nerve appears to have emerged onto the roof of the otic region just behind the hyomandibular facet and beneath the rim of the intertemporal ($frla_2$, Figs 6, 11). The dorsal limit of the spiracular groove (spig, Fig. 13) lies in front of the hyomandibular facet, posterior to the postorbital process (por) and the otic nerve (fotn, Figs 12, 13) emerged through its medial wall. In *Kansasiella* (Poplin 1974: fig. 12) and *Pteronisculus* (Nielsen 1942: fig. 12) the otic nerve passed into the spiracular canal. There are two further foramina in the posterior face of the otic region. The more lateral, smaller foramen leads into the lateral cranial canal (fv, Fig. 11); the more medial foramen (dend, Fig. 11) housed the blind-ending endolymphatic duct. From it a gutter runs down towards the cavity occupied by the sinus superior (Fig. 26). There is a recess in the roof of the otic region (rsoc, Fig. 11) which marks the anterior limit of the posterior fontanelle. In *Pholidophorus bechei* (Patterson 1975: fig. 65) the membranous extension of the supraoccipital bone enters this recess.

The lateral face of the otic region has a complex relief (Figs 4, 5, 6, 13). Anterodorsally there is a prominent postorbital process which forms the anterior boundary of the wide spiracular groove (spig, Fig. 13). This groove passes ventromedially, crosses the otico-sphenoid fissure (fos), continues on the basisphenoid behind the basipterygoid process and fades out on the parasphenoid at the level of the bucco-hypophysial canal (bhc, Fig. 50). There is no post-temporal fossa and this is considered primitive for actinopterygians. The post-temporal fossa is also missing in all other palaeoniscids, *Polypterus* and *Lepisosteus*, but occurs in caturids, semionotids, pycnodonts, *Amia*, pachycormids, pholidophorids and most other teleosts (Patterson 1975: 395).

The hyomandibular facet (fhm, Fig. 13) lies obliquely across the lateral commissure and is not lined by perichondral bone. Ventrally the facet extends onto the roof of the jugular canal (Figs 4, 5, 6). Behind the hyomandibular facet is an extensive raised area of bone, triangular in outline

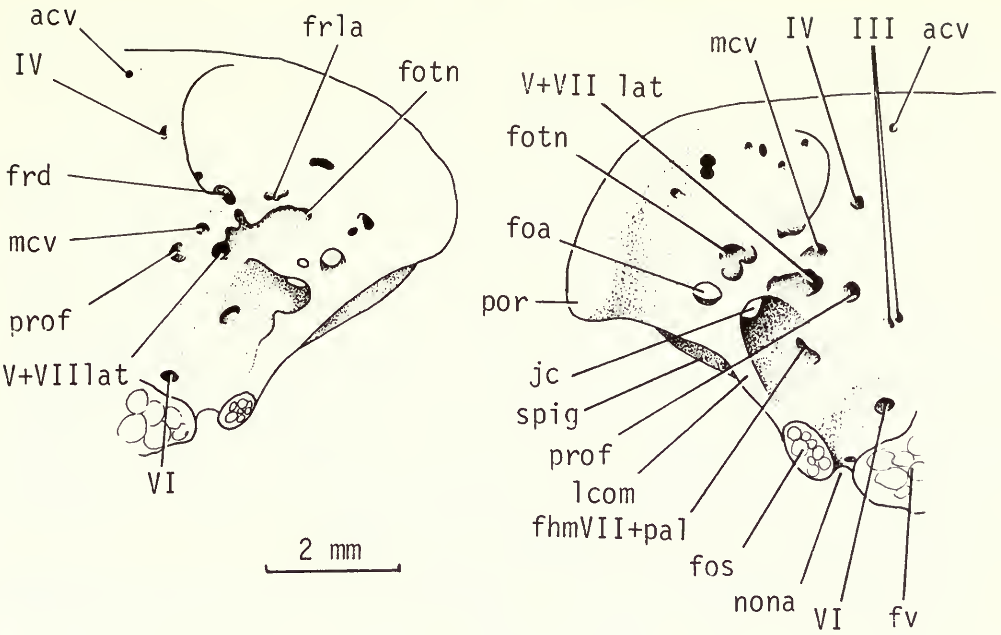

Fig. 19 *Mimia toombsi* Gardiner & Bartram. Otic and orbitotemporal regions of neurocranium in anterior view, as if cut through the middle of the orbit, from BMNH P.53234. (A), right side of the rear of the orbit; (B), left side of orbit.

with a groove or gutter dissecting it posteriorly. This area, which marks the point of origin of the dorsal hyoid constrictor muscle (oahm, oaop, Figs 4, 5, 6), stretches from the hyomandibular facet to the occipital fissure. Presumably the posterior portion of this constrictor muscle served for the adduction of the operculum (oaop, Figs 4, 5, 6) while the anteriormost region served for the adduction of the hyomandibula (oahm, Fig. 6).

Below the area of origin of the dorsal hyoid constrictor muscle a well-marked jugular groove (jg, Fig. 6) runs horizontally across the lateral face of the otic region. Behind the parampullary process (pamp, Fig. 6) the groove turns dorsolaterally in front of the vagus canal where it received the posterior cerebral vein from the upper division of that canal (gpcv, Fig. 11). The supratemporal branch of the vagus nerve (gst.X, Fig. 4) passed forward beneath the parampullary process, in the posterior portion of the jugular groove, then turned upwards and ran in a short groove through the area of origin of the dorsal hyoid constrictor muscle (gst.X, Fig. 5) and out onto the dorsal surface. Immediately beneath the posterior portion of the jugular groove there is often a further groove which soon fades out anteriorly. This groove transmitted the pharyngeal branch of the vagus nerve (gph.X, Fig. 4). The glossopharyngeal foramen (IX, Figs 4, 5, 6, 7, 13) lies either in the jugular groove or a little below it. The supratemporal branch of the glossopharyngeal nerve passed upwards from this foramen, through a distinct channel (gst.IX, Fig. 14) in the area of origin of the dorsal hyoid constrictor muscle to enter a foramen (fst.IX, Figs 4, 5, 6) immediately beneath the dermal skull roof. In some specimens this channel is confluent with that for the supratemporal branch of the vagus nerve (BMNH P.56501, P.56496, Figs 4, 6, 14), whereas in others (BMNH P.53234, Fig. 5) it is separate.

Below and in front of the glossopharyngeal foramen the wall of the saccular recess is inflated. This inflation terminates in the vestibular fontanelle (vfon, Figs 14, 15). More dorsally the ampulla of the posterior semicircular canal causes in the lateral wall a distinct swelling which is often drawn out into a prominent, ventrally-facing, parampullary process (pamp, Fig. 6) to which the first suprapharyngobranchial was presumably ligamentously attached. In earlier reconstructions (Gardiner 1973: fig. 1) I erroneously assumed that the first suprapharyngobranchial articulated at the level of the glossopharyngeal foramen.

The lateral commissure is short and broad and composed entirely of cartilage bone. A well-marked groove (goa, Fig. 15) runs dorsolaterally from the region of the orbitonasal artery foramen up into the jugular canal. Occasionally a narrow strut of bone encloses the top of this groove (BMNH P.53234, Fig. 5). In life this groove housed the orbital artery. The orbital artery passed into the jugular canal then out into the orbit by way of one or more dorsolateral foramina (foa, Figs 16, 17, 19, 20). Immediately behind the ventral portion of this orbital artery groove there is an area devoid of perichondral bone (aip1, Figs 13, 14, 15, 20). This area, which is directed anteroventrally, was the articulation for the first infrapharyngobranchial.

The foramen for the orbitonasal artery (fona, Figs 15, 50) is formed by two notches within the basisphenoid (nona, Figs 23, 24) and basioccipital (nona, Figs 16, 19, 20). This foramen transmitted the orbitonasal artery up into the floor of the orbit (Gardiner & Bartram 1977: 230). Lateral to this foramen the junction between the presumed prootics and basisphenoid remained cartilage-filled, as the otico-sphenoid fissure, which is found in most specimens (fos, Figs 13, 15). In one specimen (BMNH P.56483; Gardiner & Bartram 1977: fig. 3) and on one side only this fissure (Gardiner 1973: 106) has been obliterated by bone.

The jugular canal is a short longitudinal canal whose posterior opening transmitted the jugular vein, orbital artery and hyomandibular trunk of the facial nerve. The medial wall of the jugular canal (prefacial commissure and pila antotica) is ossified and there are separate facial, lateralis, trigeminal and profundus foramina. The geniculate ganglion lay in the funnel-like opening of the facial canal (fhm.VII + pal, Figs 16, 17, 19, 20, 21, 22) in the floor of the jugular canal and was clearly extracranial. From the geniculate ganglion the palatine nerve passed down into the back of the orbit and through the palatine fenestra (fpal, Fig. 20) while the hyomandibular trunk passed back laterally in the floor of the jugular canal. Dorsal to the facial canal and posterolateral to the trigeminal canal is a separate foramen (VII.lat, Figs 18, 22) which is presumed to have transmitted the lateralis branches of the facial nerve. The corresponding lateralis ganglion would have lain alongside the geniculate in the extramural chamber which opens in front of the jugular canal (V + VII.lat, Fig. 19). In some specimens distinct grooves pass from the mouth of the lateralis canal to the otic nerve foramina (fotn, Fig. 20) and to the foramen of the ramus lateralis accessorius (frla, Figs 20, 22), whereas in others (BMNH P.53234) bridges of bone convert parts of these grooves into canals (cf. Figs 17, 19). The internal opening of the lateralis canal (VII.lat, Fig. 18), which lies in the anterior opening of the utricular recess, is smaller in diameter than the internal openings of the facial and trigeminal canals. The facial canal (fhm.VII + pal, Figs 18, 26) originates outside the utricular recess and below the bridge of bone which separates the trigeminal from the lateralis root.

The external opening of the trigeminal canal (V, Fig. 22) is medial to the lateralis canal and dorsal to the facial canal. The opening is anteriorly-directed and lies in front of the jugular canal. The internal opening is twice as large as that of the facial canal and originates in front of the utricular recess. A bridge of bone internally (br, Fig. 18) separates the trigeminal root from the lateralis root. There is a separate canal for the profundus nerve (prof, Fig. 18) which originates in the anterior wall of the trigeminal canal and opens medial to the trigeminal foramen (prof, Figs 16, 19, 20, 22). Medial to the profundus foramen are two further foramina lying one above the other (III, Figs 16, 19, 20, 21); these presumably served for the two main branches of the oculomotor nerve. In two specimens only (BMNH P.56485, Fig. 22; BMNH P.53249, Fig. 25) there is a single, large oculomotor foramen as in most other actinopterygians.

The basisphenoid region (Figs 22, 23, 24) consists of a hollow vertical pillar which flares dorsally to join the orbital surface at the level of the oculomotor foramen. The basisphenoid forms the lateral and posteroventral margins of the pituitary fossa (pitf, Fig. 26) and the large hypophysial recess is open both dorsally and anteriorly. Ventrally, in the foot of the pillar, this recess leads to a narrow bucco-hypophysial canal (bhc, Fig. 26) which passes through the parasphenoid into the roof of the mouth (bhc, Fig. 50). Immediately behind the hypophysial

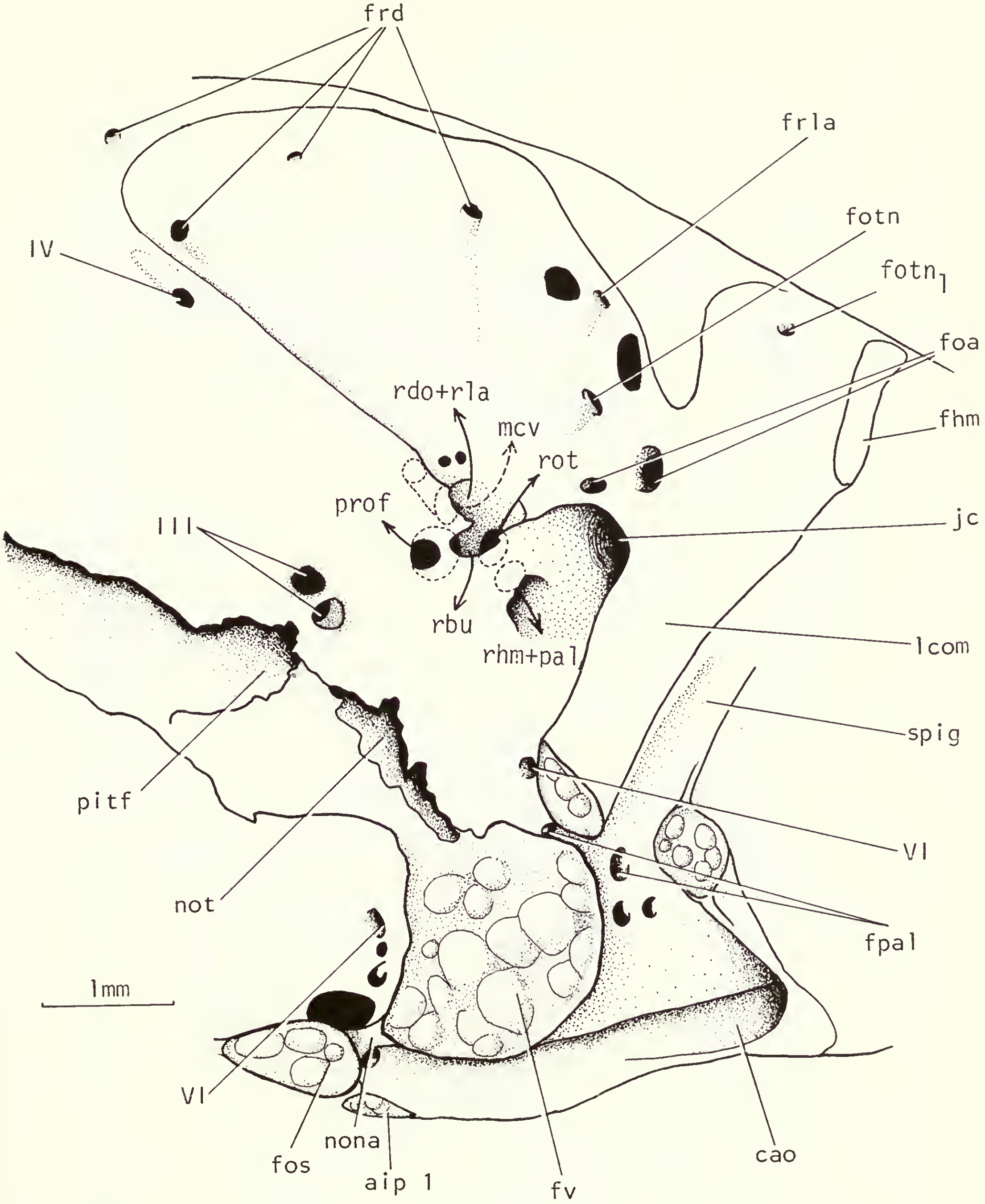
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Fig. 20 *Mimia toombsi* Gardiner & Bartram. Braincase in anterodorsal view, looking up into the rear of the orbit from the left side, from BMNH P.53259. Basisphenoid missing. The arrows depict the courses of the nerves and vessels as they passed into the orbit.

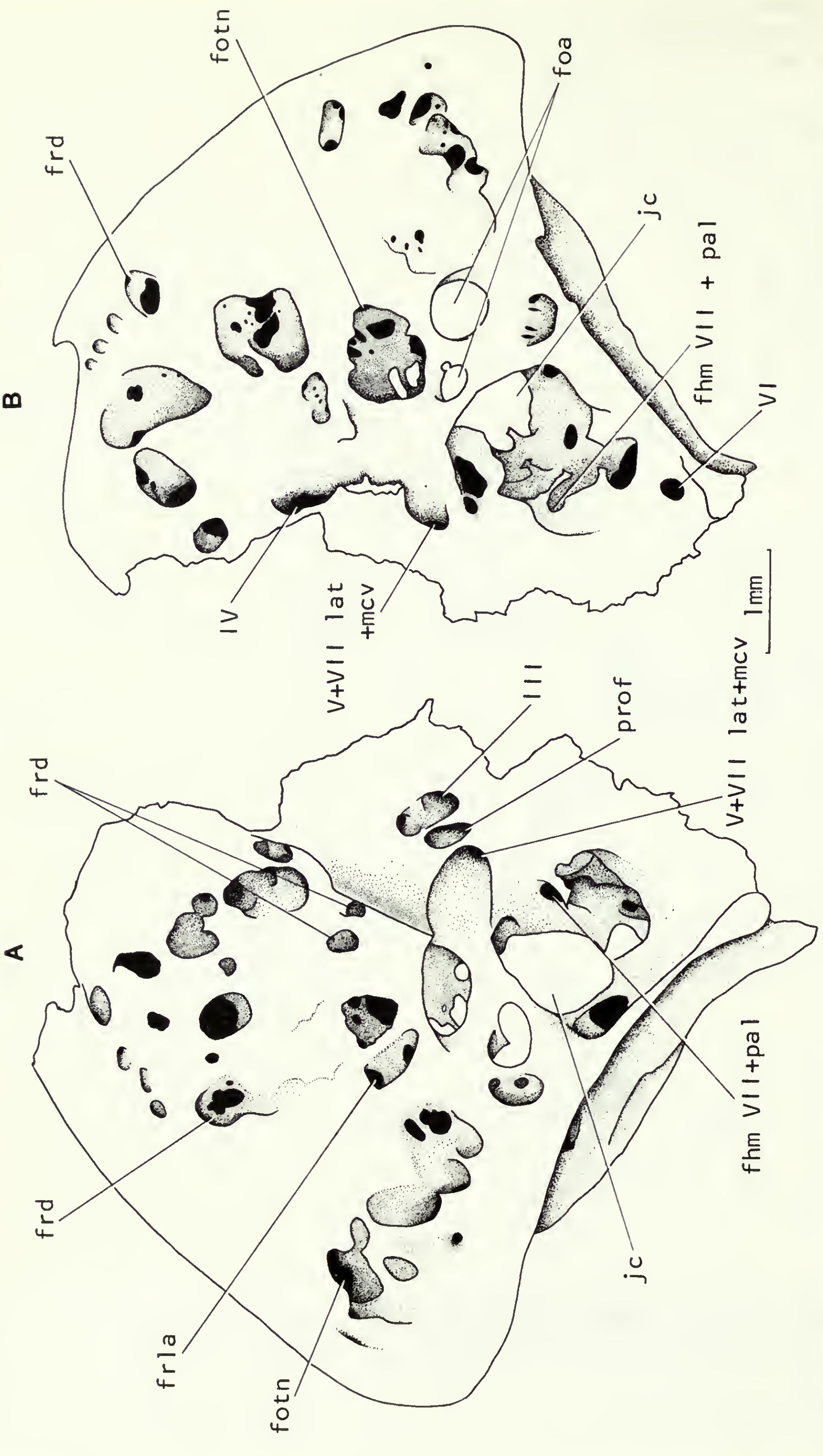
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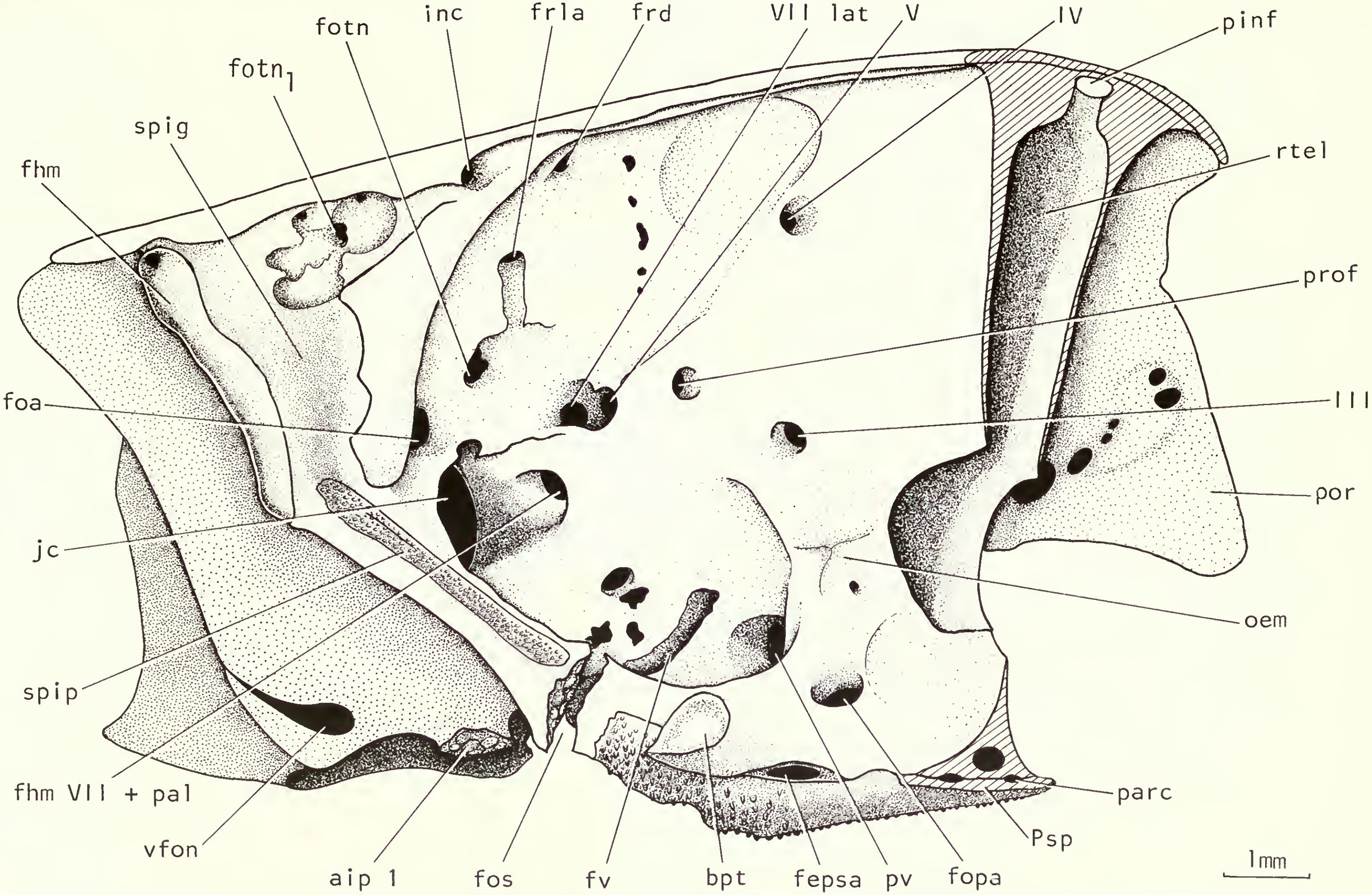
Fig. 21 *Mimia toombsi* Gardiner & Bartram. Preserved parts of the neurocranium in anterior view, from BMNH P.53245. (A), Right orbitotemporal region; (B), left orbitotemporal region.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fepsa
pv
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parc
Psp
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Fig. 22 *Mimia toombsi* Gardiner & Bartram. Otic and orbitotemporal regions of neurocranium in oblique right anterolateral view, and as if cut through the orbit, from BMNH P.56485.

recess, in the foot of the basisphenoid pillar, ran the pituitary vein (pv, Figs 22, 23, 26). Anteriorly the space for the pituitary vein is confluent with the hypohysial recess (Fig. 23). The dorsum sellae (prob, Figs 25, 26), which forms the roof of the pituitary vein canal, is presumed to be ossified by the basisphenoid. The posterior wall of the pituitary canal is expanded into a short, stout pillar (cf. Fig. 23) which flares dorsally into the dorsum sellae. Anterodorsal to the pituitary vein canal, in the anterior surface of the dorsum sellae, is a cup-shaped depression (svr, Fig. 26). This housed the saccus vasculosus, and a median canal connecting the depression with the pituitary vein canal presumably served for the passage of the saccus vasculosus vein.

Immediately in front of the ventral otic fissure and after giving off the orbitonasal artery the internal carotid arteries entered the parabasal canal (fica, Fig. 1) in the floor of the basisphenoid. Although the parabasal canal (parc, Fig. 22) runs the whole length of the basisphenoid (between it and the parasphenoid) and opens anteriorly into the roof of the mouth, only the posterior, enlarged portion, between the ventral otic fissure and the basipterygoid process, housed the internal carotid artery. The internal carotid arteries (Gardiner & Bartram 1977: figs 5, 6), after passing through this enlarged posterior portion of the parabasal canal, turned upwards and ran in a vertical canal in the anterior portion of the basisphenoid pillar ($fica_2$, Fig. 23) to enter the cranial cavity through the pituitary fossa ($fica_2$, Figs 24, 26). In some specimens (BMNH P.56501; Gardiner & Bartram 1977: fig. 6) the internal carotid briefly ran in a groove in the lateral wall of the basisphenoid pillar, and gave rise to an anterior branch which ran anteroventrally towards the snout in a short groove on the dorsal surface of the basisphenoid before passing down into the palatine (parabasal) canal. The palatine nerve entered the parabasal canal through an anteroventrally-directed foramen ($fpal_2$, Figs 23, 24), immediately in front of the ventral otic fissure, and presumably ran the entire length of the parabasal canal before emerging in the roof of the mouth at the level of the vomers. It was probably accompanied anteriorly by the palatine artery and vein.

Just in front of the basipterygoid process a short canal runs laterally from the parabasal canal to open above the edge of the parasphenoid (fepsa, Figs 13, 22, 50). This carried the efferent pseudobranchial artery which, after its anastomosis with the internal carotid (Gardiner & Bartram 1977: figs 5, 6), turned upwards and forwards through a distinct foramen (fopa, Figs 13, 22, 23, 24) into the floor of the orbit as the ophthalmic artery.

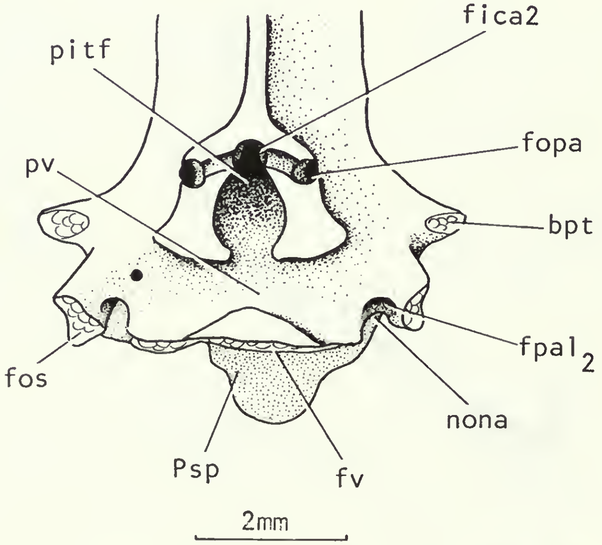


Fig. 23 *Mimia toombsi* Gardiner & Bartram. Posterior basisphenoid region of braincase cut horizontally at level of pituitary vein, in dorsal view, from BMNH P.56504.

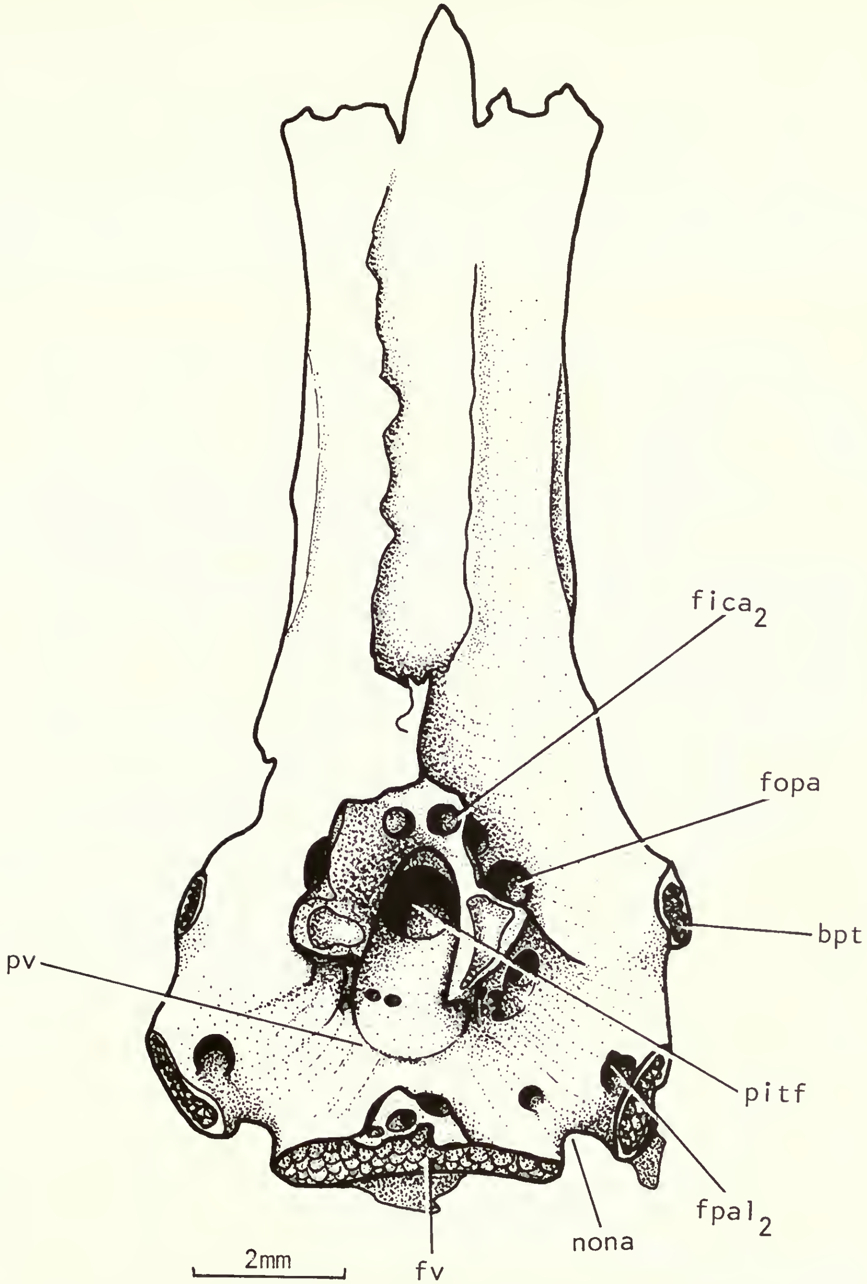


Fig. 24 *Mimia toombsi* Gardiner & Bartram. Preserved parts of basisphenoid in dorsal view, from BMNH P.53225.

On the lateral wall of the basisphenoid pillar, dorsal to the ophthalmic artery foramen, is a pronounced cup-shaped depression, divided into three components by prominent ridges (oem, Fig. 22; see also Gardiner & Bartram 1977: fig. 6). This depression must have housed at least three of the rectus muscles, but since there is not even a hint of a myodome the origin of the fourth (external) rectus muscle can only be guessed at. Perhaps it also was attached to the lateral wall of the pillar.

The posteroventral floor of the orbit behind the ventral otic fissure has smoothly curved walls in the area of the facial foramen, but in front of the anteroventrally-directed canal for the abducens nerve (VI, Figs 16, 19, 20, 21) it is often incompletely ossified and frequently fenestrated (cf. Fig. 22). This is the area where the external rectus muscle might be expected to originate. In the floor of this area there is often a short canal for the palatine nerve (fpal, Fig. 20).

Above the jugular canal the walls of the orbital face consist of smooth bone only interrupted by a distinct ridge running up towards the roof of the orbit from the trigeminal foramen. This ridge passes posterior to the foramen for the trochlear nerve (IV, Figs 13, 16, 17, 19, 20, 21, 22). Laterally the walls flare out to meet the postorbital processes and dorsally they meet the

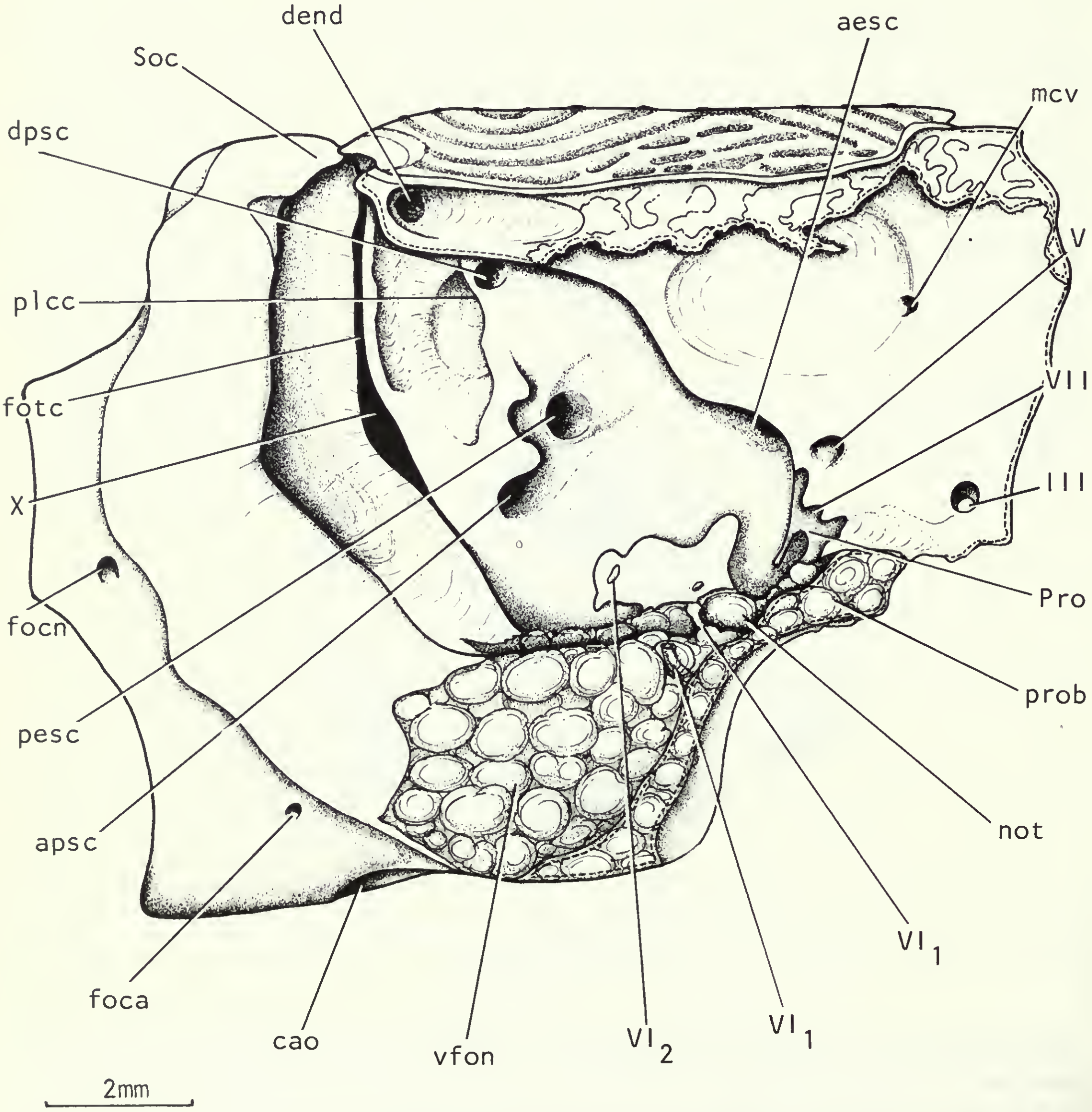


Fig. 25 *Mimia toombsi* Gardiner & Bartram. Preserved post-ethmoid part of neurocranium in left anterolateral view, from BMNH P.53249.The right otico-orbitotemporal wall is missing; dotted lines indicate broken surfaces.

frontals. The two walls come very close together in the mid-line (cf. Fig. 16) and are scarcely separated by the small, median optic fenestra (II, Fig. 13).

A further foramen (mcv, Figs 18, 20) opens into the roof of the recess for the lateralis and geniculate ganglia. From this foramen a canal passes anterodorsally to open on the internal surface above the saccular recess and behind the trochlear foramen (mcv, Figs 18, 25, 26). This canal must have transmitted the middle cerebral vein. In one specimen (BMNH P.53234, Fig. 19) the canal opens above the ganglion recess. Anterior to the ramus lateralis accessorius foramen there is a series of up to four foramina (frd, Figs 20, 21, 22), which transmitted branches of the superficial ophthalmic nerves to the neuromasts of the supraorbital canal (crd, Figs 33,

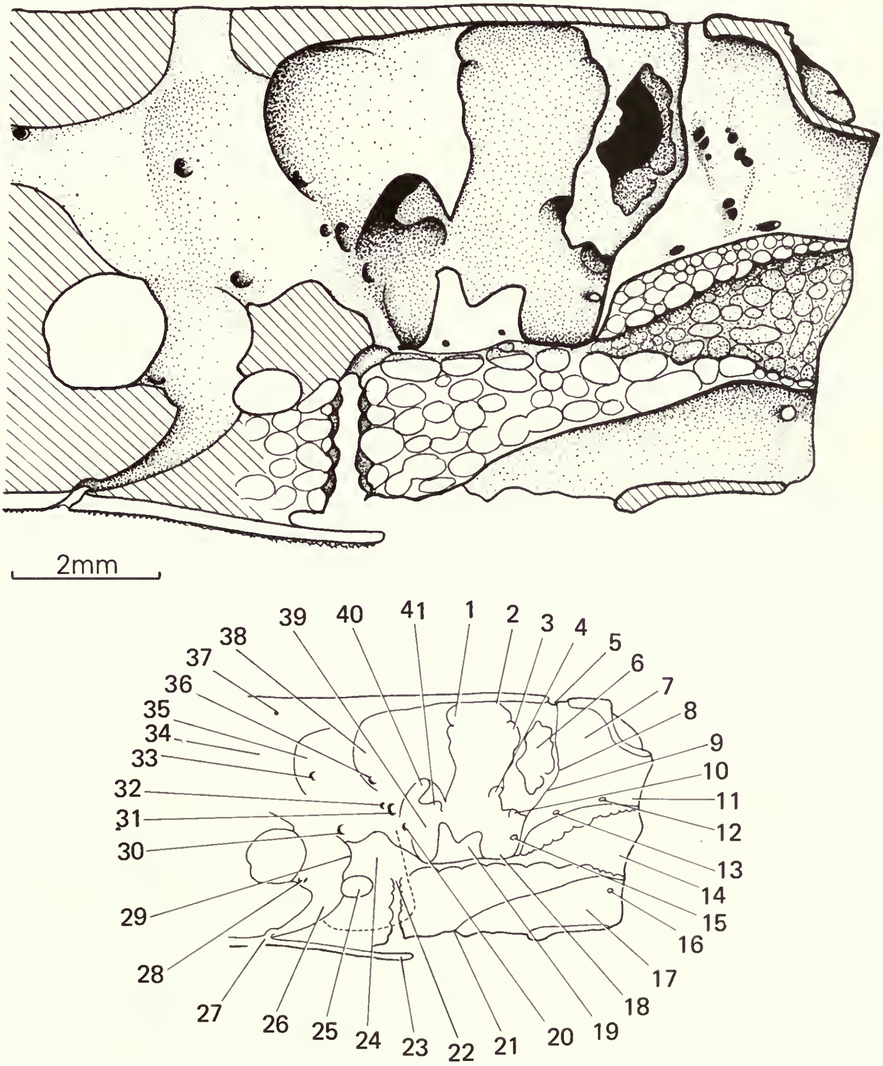


Fig. 26 *Mimia toombsi* Gardiner & Bartram. Post-ethmoid portion of neurocranium and parasphenoid in sagittal section, from the left side, based on BMNH P.53234. From Gardiner & Bartram (1977). Key (diagram below): 1, dasc; 2, dpsc; 3, ssu; 4, pesc; 5, pdf; 6, plcc; 7, rmye; 8, fotc; 9, X; 10, apsc; 11, fm; 12, focn; 13, fboca; 14, not; 15, IX; 16, foca; 17, cao; 18, sacr; 19, Z; 20, fhm.VII; 21, alig; 22, fv; 23, Psp; 24, prob; 25, pv; 26, pitf; 27, bhc; 28, fica$_2$; 29, svr; 30, III; 31, VII.lat; 32, V; 33, IV; 34, rtel; 35, ropl; 36, mcv; 37, acv; 38, rmet; 39, utr; 40, aasc; 41, aesc.

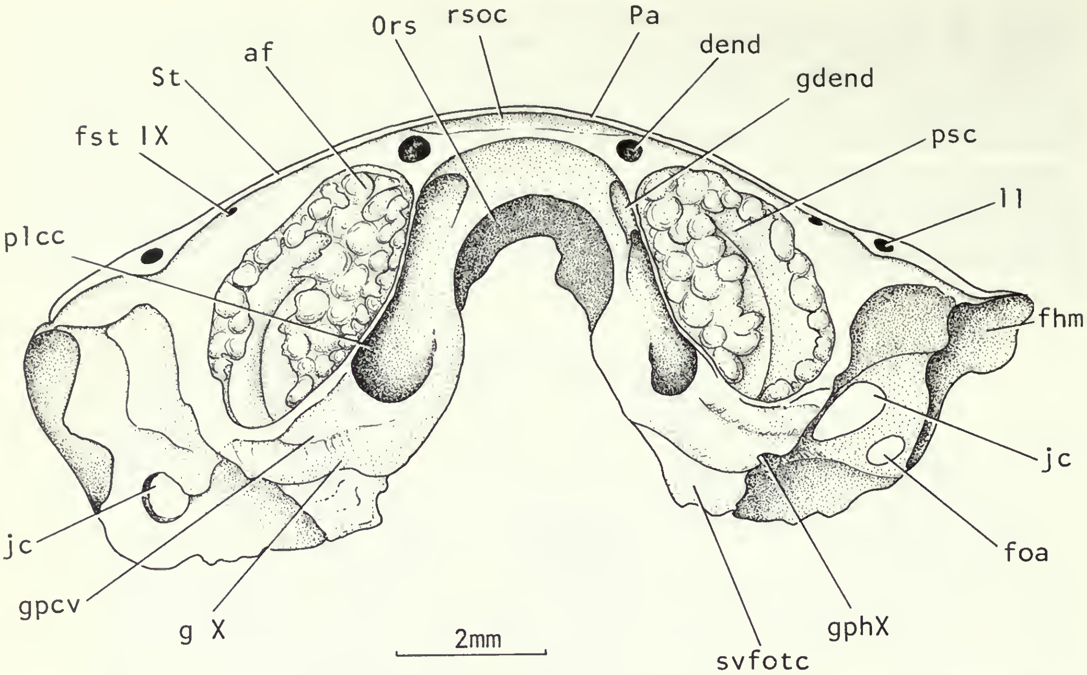


Fig. 27 *Moythomasia durgaringa* Gardiner & Bartram. Dorsal portion of otic and orbitotemporal regions of neurocranium and attached dermal bones in posterior view, from BMNH P.53227.

34). In some specimens (BMNH P.56504, Fig. 17) these branches were contained for part of their orbital course within a short canal, while in others (BMNH P.53234, P.53245, Figs 19, 21A) these branches passed up through the rim of the lateralis ganglion recess before passing out over the orbital surface and into the four dorsal foramina.

The foramen for the anterior cerebral vein (acv, Figs 13, 14, 16, 19) opens into the roof of the orbit just behind the dorsal anterior myodome (amyd, Fig. 13). It passes medially and originates in the recess housing the telencephalon (Fig. 26). Occasionally this vein was developed on the left side only (cotel, Figs 33, 34) as in the specimen of *Kansasiella* described by Poplin (1974: fig. 22) and in the *Latimeria* dissected by Robineau (1975: fig. 1A). The olfactory nerves were sheathed by perichondral bone (I, Figs 16, 33, 34, 35), but a small gap in the roof of the olfactory canal (gI, Fig. 13), where it passes beneath the floor of the dorsal anterior myodome, affords communication with the orbit.

The brain is assumed to have been closely enveloped by bone, rather more completely than in other palaeoniscids, and if so its shape and size may be accurately deduced. The relief of the brain cavity is shown in sagittal section (Fig. 26), and the dorsal extent of the cranial cavity in Figures 33, 34. The anterior dorsal fontanelle is reduced to the pineal foramen (pinf, Figs 16, 33, 34) which opens into that part of the cranial cavity which accommodated the diencephalon; the complete closure of the anterior dorsal fontanelle in adults is considered a primitive osteichthyan feature. Anterior to the diencephalon the cranial cavity is less broad where the telencephalon was housed (ctel, Figs 33, 34; rtel, Fig. 26). Anteriorly this telencephalic cavity may be overlain by inpushing of that part of the orbital wall (Pl. 1; amyd, Fig. 33) which delimits the dorsal anterior myodomes.

Posterior to the pineal foramen there is a marked increase in the breadth of the cranial cavity (copl, Fig. 33). In sagittal section this appears as a marked, rounded depression (ropl, Fig. 26) from which the trochlear nerve (IV) passed anteriorly into the orbit. This depression, which is medial to the postorbital process, contained the large optic lobe from which the optic nerves

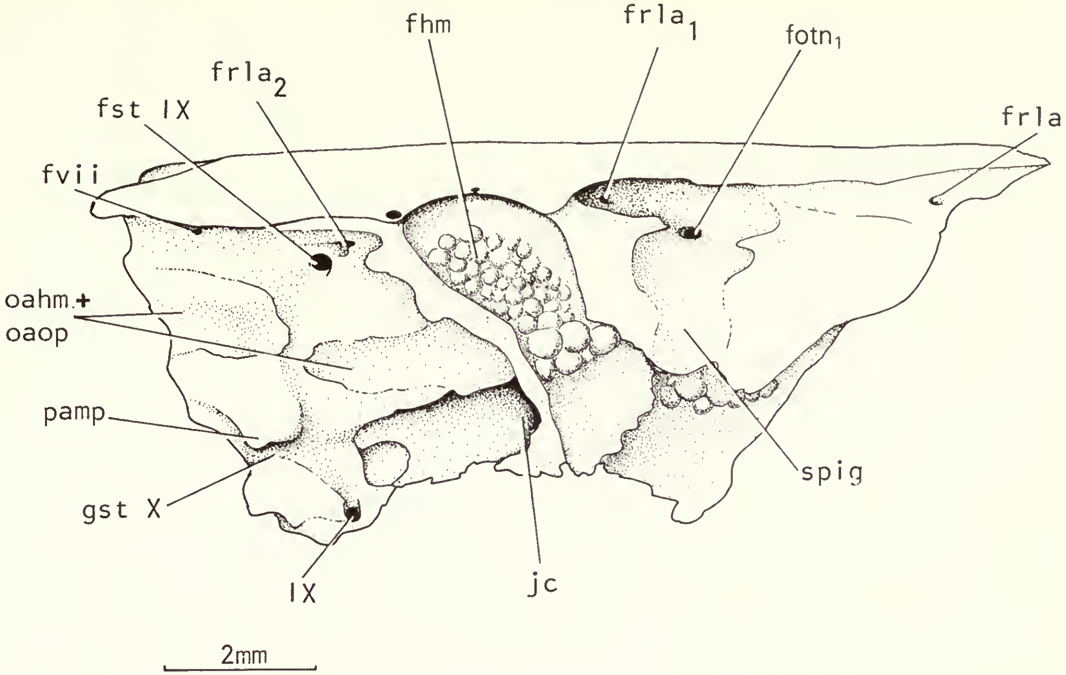


Fig. 28 *Moythomasia durgaringa* Gardiner & Bartram. Dorsal portion of otic and orbitotemporal regions of neurocranium and attached dermal bones in right lateral view, from BMNH P.53227.

passed out anteroventrally through the optic fenestra (II). The cranial cavity beneath the optic lobes decreases rapidly in breadth and is floored by the 'prootic' bridge (dorsum sellae, prob, Fig. 26). The walls in this region are perforated by the oculomotor foramen (III) and the floor in front of the 'prootic' bridge by the pituitary fossa (pitf, Fig. 26). A further strong depression (rmet, Fig. 26) behind the optic lobes and above the anterior ampullary chamber (aasc, Fig. 26) and utricular recess (utr, Fig. 26) accommodated the cerebellum. The middle cerebral vein (mcv) left the anteroventral corner of this depression on its way to the orbit. Below the cerebellum the walls of the cranial cavity decrease in breadth much as beneath the optic lobes and are perforated by the foramen for the trigeminal plus profundus nerves (V, Figs 18, 26) and the foramen for the hyomandibular and palatine trunk of the facial nerve (fhm.VII + pal, Fig. 18). The lateralis branch of the facial nerve (VII.lat, Figs 18, 26), however, passed out through the front of the recess for the utriculus (utr, Figs 18, 26).

There is a wide communication between the cranial and labyrinth cavities, as in other palaeoniscids, *Polypterus, Acipenser, Lepisosteus* and *Amia*. Nevertheless the labyrinth cavity is mostly enclosed within the bony walls of the otic region. The saccular recess is extensive and in the form of an almost square pocket similar in size and shape to that of *Pteronisculus* (Nielsen 1942: fig. 14) but deeper than in *Pholidophorus* (Patterson 1975: fig. 66). Although this pocket is in wide communication with the cranial cavity above, the zygal plates (Z, Fig. 26) form an inner, dorsal wall to the pocket separating it (and the contained sacculus) from the floor of the brain.

From the serial sections it can be seen that a single otolith is present in each saccular recess. It appears to be longer than deep and relatively compact. The glossopharyngeal nerve passed through the dorsoposterior part of the saccular recess. Immediately above the glossopharyngeal foramen (IX, Fig. 26) and below the opening of the lateral cranial canal there is a deep recess which housed the ampulla of the posterior semicircular canal (apsc, Figs 25, 26). The sinus superior lay in front of and medial to the opening of the lateral cranial canal in a distinct concavity (ssu, Fig. 26) in the cranial wall. Ventrally, in the region of the recess for the posterior ampullary chamber, a flange of bone forms a partial posterior boundary to the sinus superior recess. A similar flange of bone is found in *Pholidophorus* (Patterson 1975: fig. 65). A dorsal opening at the front of the ampullary recess marks the exit of the external semicircular canal. Thus this canal must have passed laterally through the anterior part of the ampullary recess as in *Kansasiella* (Poplin 1974: fig. 20), *Perleidus, Ospia, Caturus* and *Pholidophorus*, whereas in other palaeoniscids such as *Pteronisculus, Kentuckia* and *Boreosomus* the openings of the posterior ampullary recess and the external canal are separated by a small pillar of bone. At the top of the groove for the sinus superior lie the dorsal openings of the anterior (dasc, Fig. 26) and posterior (dpsc) semicircular canals. The anterior semicircular canal is considerably longer than the other two canals and anteriorly enters its ampulla (aasc, Figs 18, 26) in the anterodorsal portion of the utricular recess. The external ampullary chamber (aesc, Figs 18, 26) lay in a posterior diverticulum of the utricular recess behind and below a well-marked projection on the posterior margin of the entrance to this recess. A similar projection has been described in *Pholidophorus* (Patterson 1975: fig. 65) and in the dipnoan *Griphognathus* (Miles 1977: fig. 10).

Between the posterior semicircular canal and the recess for the sinus superior is an intramural lateral cranial canal (lcc, Fig. 12). Posteriorly this canal opens into the cranial cavity (plcc, Figs 12, 25, 26) above the posterior ampullary recess and in front of the occipital fissure. This lateral cranial canal (Jarvik 1980) is reduced to a small pocket in many specimens, where it is similar in extent to that described in *Kentuckia* (Rayner 1951: fig. 9, X) and *Kansasiella* (Poplin 1974: fig. 20, elmy). In other less well ossified specimens the canal is more extensive (Fig. 12) and may even communicate with the cranial cavity anteriorly (in front of the sinus superior) by several small foramina. In other individuals the roof of the canal is fenestrated and widely open dorsally. A lateral cranial canal is present in most palaeoniscids, Recent chondrosteans, *Perleidus, Lepisosteus*, most halecomorphs, pholidophorids and leptolepids.

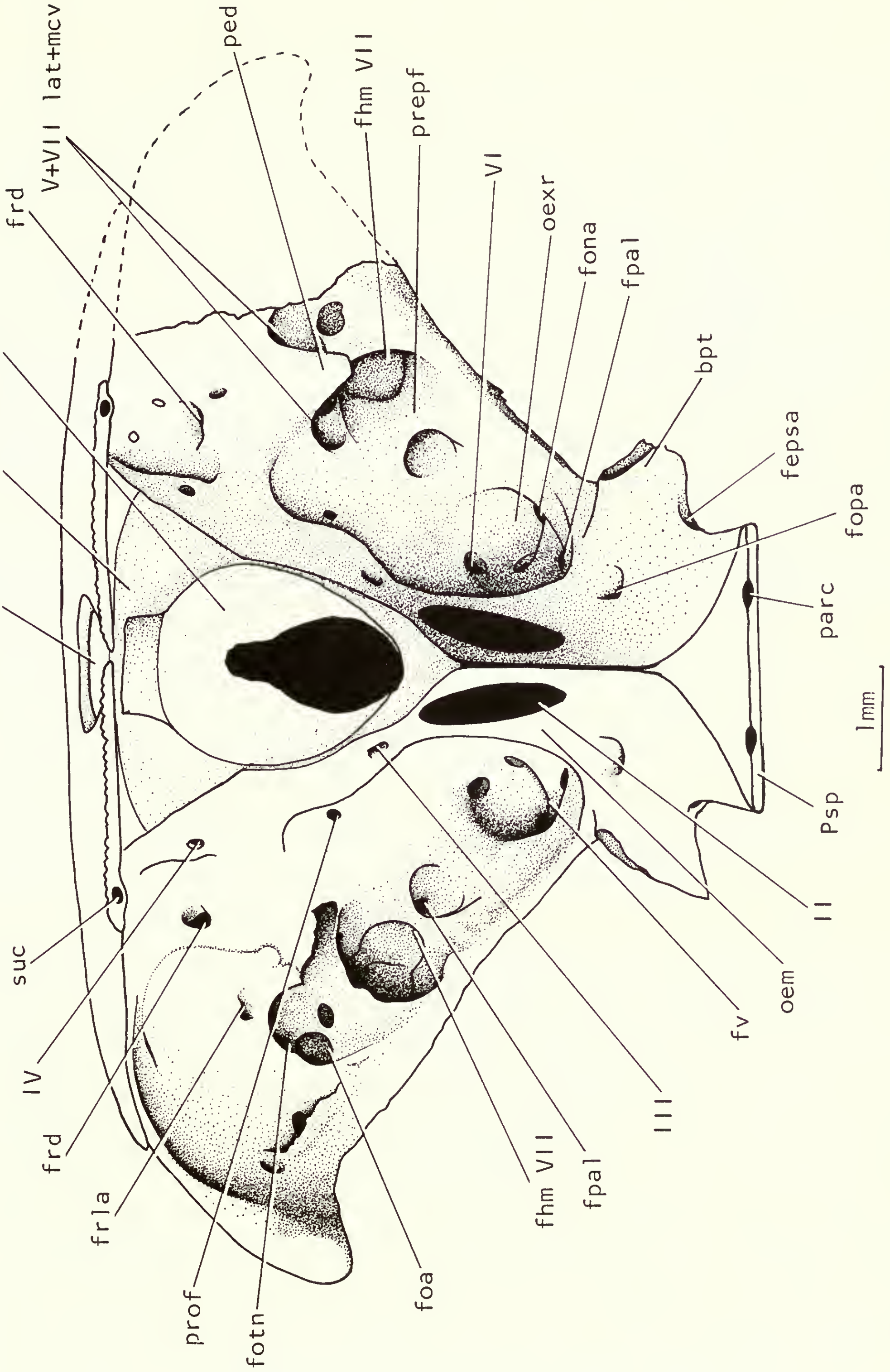
The sclerotic ring is well preserved and usually consists of either a complete ring or two segments, each comprising three separate layers of bone. The outer layer is dermal and ornamented with ridges of ganoine which run more or less concentrically round the ring (BMNH P.56483), whereas the underlying layers (inner and outer) are made up of very thin perichondral bone (BMNH P.56496). Where there are two segments the two halves are disposed dorsally and ventrally, not fore and aft of the eyeball as in teleosts and fossil halecomorphs. In one specimen of *Mimia*, however, there are three separate segments and in another, presumably a juvenile (BMNH P.53258), there are four separate plates. The innermost part of the sclerotic is ossified as a thin, perichondral, basal sclerotic bone around the entry of the optic nerve and vessels (BMNH P.53228). This basal sclerotic bone is cup-shaped and like the outer perichondral layer which underlies the dermal ring, has a corresponding inner layer of perichondral bone. Thus, bone is developed on both surfaces of the sclerotic cartilage as in other primitive actinopterygians (Patterson 1975: 415), placoderms and agnathans (see p. 253).

Moythomasia durgaringa

The posterior face of the otic region is only partially lined with perichondral bone. A large ovoid area (af, Fig. 27), stretching from just above the vagus canal almost to the opening of the endolymphatic duct, has no perichondral lining and must have been cartilage-filled during life. A similar loss of the perichondral lining is presumed to have occurred early in the phylogeny of dipnoans and osteolepiforms (Gardiner 1973: 111). A notch (gph.X, Fig. 27) in the groove for the vagus nerve served for the passage of the pharyngeal branch of that nerve as in some specimens of *Mimia*, but the foramen for the endolymphatic organ (dend) is considerably larger than the corresponding foramen in *Mimia*. The lateral face of the otic region (Fig. 28) only differs from that of *Mimia* in the more ventral position of the raised areas for the origin of the dorsal hyoid constrictor muscle (oahm + oaop).

The jugular canal is a trifle longer than in *Mimia* and the orbital artery entered posteriorly by a separate vertical canal (goa, Fig. 7). In one specimen (BMNH P.53227, Fig. 31), in which the orbital region is broken open, the individual canals for the various nerves opening into the jugular canal can be recognized as distinct tubes of perichondral bone.

The facial canal (VII, Fig. 31), which transmitted the palatine and hyomandibular trunk of the


V+VII lat+mcv
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fv
III
fpal
fhm VII
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fotn
prof
frla
frd
IV
suc
pinf
copl
ctel
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Fig. 29 *Moythomasia durgaringa* Gardiner & Bartram. Preserved parts of neurocranium and attached roofing bones in anterior view, from BMNH P.53255.

facial nerve, opens into the ventromedial corner of the orbital opening of the jugular canal. This external opening is confluent with a palatine fenestra (fpal, Fig. 29) in which the geniculate ganglion must have lain. Thus *Moythomasia* is unique amongst palaeoniscids in possessing a prepalatine (or prefacial) floor (prepf, Fig. 29) to the jugular canal.

Lying immediately above the facial canal the lateralis canal (VII.lat, Fig. 31) opens together with the trigeminal canal (V, Fig. 31) into a large pocket in the mouth of the jugular canal, dorsal to the palatine fenestra. This pocket must have housed both the lateralis and gasserian ganglia. Two grooves in the medial wall of this pocket run upwards from the mouth of the lateralis canal. One of the grooves passes up towards the foramen for the otic nerve and must have transmitted the otic branch (rot, Fig. 31), while the more medial groove served for the dorsal branch of the superficial ophthalmic nerves and the recurrent branch of the facial nerve (rdo + rla). From this medial groove the ophthalmic and recurrent branches entered a short canal to re-emerge in the back of the orbit (frd, Fig. 29) before finally entering separate foramina in the orbital roof (frla, frd, Fig. 30). The trigeminal canal runs dorsal to the lateralis canal with the canal for the profundus (prof) running anterior to both. The profundus canal has a separate internal opening, whereas externally it opens in front of the pocket for the gasserian and lateralis ganglia (prof, Figs 29, 30). A pedicel of bone (ped, Figs 29, 30) often covers this pocket and is homologous with the pterosphenoid pedicel in *Amia* and *Pholidophorus*. In some specimens (BMNH P.56480, Fig. 30) it is complete and spans the mouth of the jugular canal. A further foramen beneath the posterior margin of the pterosphenoid pedicel is presumed to have transmitted the middle cerebral vein (mcv, Fig. 31).

The internal carotid artery, after passing through the enlarged posterior portion of the parabasal canal, turned upwards to emerge in the floor of the orbit in the foot of the basisphenoid pillar (fopa, Figs 7, 32), from whence the ophthalmic artery ran forwards along the

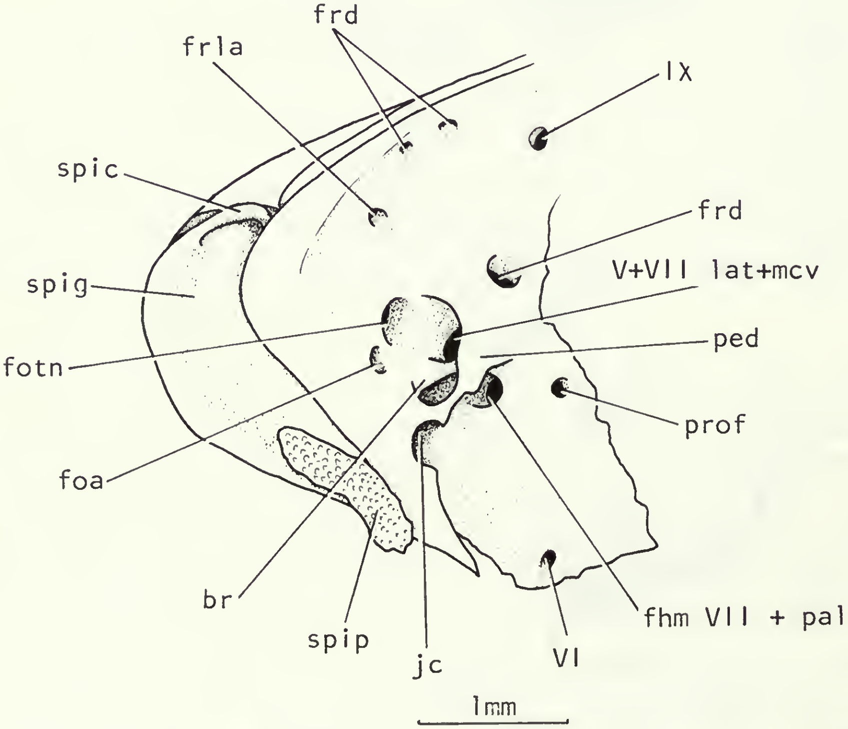

Fig. 30 *Moythomasia durgaringa* Gardiner & Bartram. Preserved part of the rear of the right orbit in oblique anterolateral view, from BMNH P.56480.

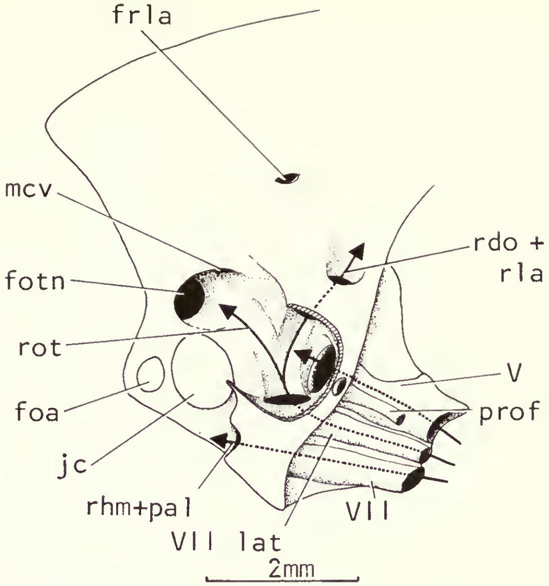

Fig. 31 *Moythomasia durgaringa* Gardiner & Bartram. Sketch of the rear of the right orbit in anterior view, from BMNH P.53227. Mouth of the trigeminofacial chamber is drawn as if cut away, and the cut surface cross-hatched. The passage of individual nerves is represented by arrows.

floor of the orbit while the internal carotid ran upwards in a groove in the anterolateral wall of the basisphenoid pillar to enter the cranial cavity through the pituitary fossa.

Muscle scars, in the form of two distinct cups, one above the other, are present on the basisphenoid bolster dorsal to the foramen for the internal carotid artery, in an identical position to those in *Mimia*. Whether or not the external rectus muscle originated here or in the back of the orbit ventrolateral to the abducens foramen (oexr, Fig. 29) could not be determined with certainty. However, the otico-sphenoid fissure is closed by bone anteriorly and laterally, where the ascending process of the parasphenoid bridges it, but posteriorly it is open for a short distance (fos, Fig. 7).

The sclerotic ring consists of two segments of dermal bone as in some specimens of *Mimia*, but no evidence of perichondral ossifications could be found. In the closely allied *Moythomasia nitida* four dermal plates have been described (Jessen 1968: fig. 12).

Otic and orbitotemporal region: discussion

1. *Parampullary process*. This is a prominent feature of the opisthotic in *Mimia* and *Moythomasia*, and is also prominent in *Kentuckia* (Rayner 1951: fig. 7), *Birgeria* (Nielsen 1949: fig. 60), '*Ambipoda*' (Beltan 1968: pl. 6) and *Australosomus* (Nielsen 1949: fig. 7). In *Polypterus* the opisthotic ossifies late in ontogeny from a centre over the base of the posterior semicircular canal and in the adult it is a large ossification with extensive membrane bone components. It has a strongly-developed ridge extending dorsoposteriorly along its length. Under this ridge the hyomandibular and opercular adductor muscles take origin and the branchial levator muscles originate more posteriorly. The posterior portion of this opisthotic ridge in *Polypterus* is taken to be the homologue of the parampullary process in palaeoniscids, and the parampullary process is taken to have developed primitively in relation to the branchial levator muscles. No parampullary process as such is present on the opisthotic of *Perleidus* or parasemionotids, though it seems likely that the branchial levator muscles must have been attached to this bone, since the intercalar is still small and has not grown over the cranial fissure. In more advanced actinopterygians the parampullary process is often difficult to recognize because that region of the opisthotic on which the branchial levator muscles originate has been captured by anteroventrally-directed membrane outgrowths from the intercalar. Thus in *Amia* the branchial levator muscles originate entirely on the membranous intercalar. Presumably most of these

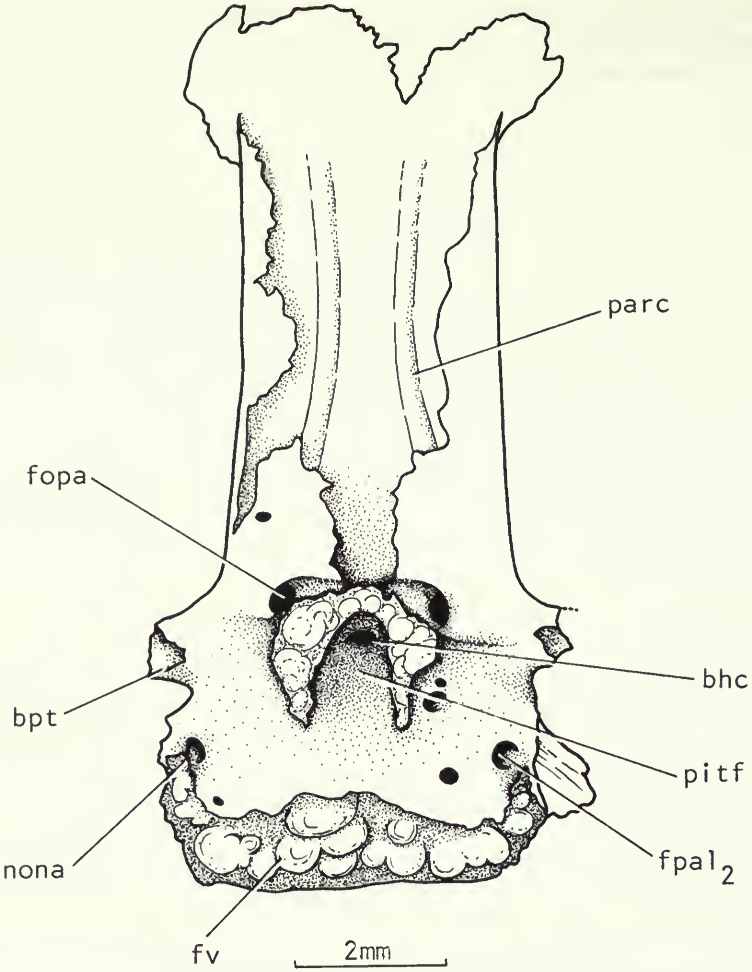

Fig. 32 *Moythomasia durgaringa* Gardiner & Bartram. Preserved parts of basisphenoid in dorsal view, from BMNH P.53219.

muscles originated on the intercalar in caturids also, but in *'Aspidorhynchus'* (Patterson 1975: fig. 99, prlm), *Macrepisteus* (Schaeffer 1971: fig. 5) and *Heterolepidotus* (Gardiner 1960: fig. 29) a knob on the surface of the prootic must have served for the origin of at least the anteriormost branchial levators.

In Devonian dipnoans the adotic process, a knob which arises from the ventral edge of the jugular groove behind the glossopharyngeal foramen, homologous with the adotic eminence of Devonian actinistians (*Nesides* Bjerring 1977: fig. 23A) and the 'process for the attachment of adductor muscles of hyomandibula' of *Eusthenopteron* (Bjerring 1971: fig. 8), is said by Miles (1977: 79) to be a similar outgrowth to the caturid prootic knob. But since the adotic process lies partly below the jugular canal it seems more likely that it received either the ventral portion of the first branchial levator muscle, which in *Polypterus* is attached to the parasphenoid, or the ceratobranchial ligament (cf. *Polypterus*, Allis 1922: 234). In pholidophorids, where the intercalar has extensive membrane bone outgrowths covering the adjacent otic bones, the parampullary process of the opisthotic can still be recognized (Patterson 1975: fig. 61, ampp). In pholidophorids and Upper Jurassic leptolepids struts of bone from the prootic and intercalar unite to form a bridge over the subtemporal fossa. *Elops* and *Osteoglossum* have a similar bridge, and here the branchial levator muscles originate, as well as the ligamentous attachment of the first suprapharyngobranchial. There is a distinct parampullary process in actinistians which is borne on the opisthotic in *Macropoma, Laugia* and *Wimania*. In the Recent *Latimeria* a cartilaginous process in an homologous position is the origin of both the branchial levator muscles and the ligament of the suprapharyngobranchial. A parampullary process may also be recognized in rhipidistians such as *Ectosteorhachis* (Romer 1937: figs 2, 4, 5, popcp ?) where its relationships to the foramina for the glossopharyngeal and vagus nerves (particularly the supratemporal branches) are exactly as in *Mimia* and *Moythomasia*. A similar process in *Eusthenopteron* (Jarvik 1954: fig. 1, prpo) also served as a point of articulation for the first suprapharyngobranchial. In the Devonian dipnoan *Griphognathus* (Miles 1977: 79) a small ventral outgrowth from the upper margin of the jugular groove, between the foramina for the vagus and glossopharyngeal nerves, may also have given origin to branchial levator muscles. No such process has been described in acanthodians, placoderms or chondrichthyans. The presence of a parampullary process on the opisthotic is presumed to be a primitive osteichthyan character.

2. *Articulation of first suprapharyngobranchial*. In the Gogo palaeoniscids there is no obvious facet for the articulation of the spatulate first suprapharyngobranchial. It rested against or articulated with the opisthotic region of the braincase in front of the parampullary process and below the jugular canal (Fig. 119). In *Polypterus*, while there is no suprapharyngobranchial as such, the first epibranchial articulates with the opisthotic below the jugular canal and in front of the glossopharyngeal foramen (Devillers 1958: 665). In sturgeons the first suprapharyngobranchial articulates with the opisthotic (when present) below the jugular canal, but the second suprapharyngobranchial articulates with the braincase above the jugular canal (Bertmar 1959: 305, 329). The first suprapharyngobranchial also articulates with the otic region in *Polyodon* (Bridge 1878). In *Amia*, as in *Polypterus*, there is no suprapharyngobranchial. In *Lepisosteus* the cartilaginous first suprapharyngobranchial does not articulate with the braincase: it lies behind the glossopharyngeal nerve. In teleosts which have retained an ossified first suprapharyngobranchial such as *Elops*, and other members of the families Elopidae and Alepocephalidae, this element inserts by a ligament together with the branchial levator muscles on the intercalar strut. The first pharyngobranchial in *Latimeria* is also in ligamentous attachment to the parampullary process (Millot & Anthony 1958) and in *Eusthenopteron* (Jarvik 1954: fig. 23) the pharyngobranchial is said to articulate directly with that process.

Elsewhere in actinopterygians the pattern is variable. In *Birgeria* (Nielsen 1949: fig. 60) the suprapharyngobranchial articulated with a distinct facet, lacking perichondral lining, on the parampullary process of the opisthotic, as in *Eusthenopteron*. On the other hand in *Pteronisculus* (Nielsen 1942: 196) the first suprapharyngobranchial articulated with a large facet lacking perichondral lining on the posteroventral portion of the opisthotic below the glossopharyngeal foramen. This articulation is below the jugular groove and is in a similar position in *Mimia, Moythomasia* and *Acipenser*. A smaller, paired articulatory surface, lying rather more anteriorly but still below the jugular canal, served for the articulation of the first suprapharyngobranchial in *Kansasiella* (Poplin 1974: fig. 13). In the pholidopleurid *Australosomus* (Nielsen 1949: fig. 37) the articulatory facet is in an identical position to that in *Pteronisculus*. In caturids (*Caturus* Gardiner 1960: fig. 36; *'Aspidorhynchus'* Patterson 1975: fig. 99, asup.1; *Heterolepidotus* Patterson 1975: fig. 102, asup.1; *Osteorachis* Patterson 1975: 397) the articular area is equally distinct, and as in *Pteronisculus, Kansasiella* and *Australosomus* lies just below the glossopharyngeal foramen, in a notch in the margin of the intercalar. Elsewhere within amioids an articulatory facet is not recognizable nor is one to be seen in semionotids, pachycormids or leptolepids. The only other recorded occurrence of a distinct facet for the articulation of the first suprapharyngobranchial is in pholidophorids, where it is said to lie below the jugular groove on the prootic, midway between the glossopharyngeal and facial foramina (Patterson 1975: 397). This position is considerably more anterior and more ventral than in any other actinopterygian, rhipidistian or actinistian. It seems likely that this facet on the prootic was not for the first suprapharyngobranchial (which was probably in ligamentous contact with the intercalar strut as in *Elops*) but for the second infrapharyngobranchial. The second infrapharyngobranchial in *Elops* lies in close proximity to the posterior portion of the prootic, with its head in a similar position to the facet described by Patterson (1975: fig. 56, asup.1) in *Pholidophorus*. The second infrapharyngobranchial also articulates with the braincase in *Acipenser* and *Polyodon* (in front of the vagus foramen) and in *Eusthenopteron* where it articulates with the basioccipital region (as does the first infrapharyngobranchial). The condition in *Eusthenopteron* is similar to *Australosomus* (Nielsen 1949: 122) except that in the latter the second infrapharyngobranchial merely lies adjacent to the underside of the basioccipital.

There are no known pharyngobranchials in dipnoans (Miles 1977: 287) but cartilaginous nodules are said to underlie the medial ends of the epibranchials in *Neoceratodus* (Nelson 1968: fig. 5D). Since no suprapharyngobranchials are known in placoderms, chondrichthyans or acanthodians they are presumed to be a derived feature of osteichthyans (Rosen *et al.* 1981; see also under branchial arches, p. 362).

3. *Articulation of first infrapharyngobranchial.* In *Mimia* and *Moythomasia* the articulation of the first infrapharyngobranchial is represented by an area devoid of perichondral lining at the posteroventral corner of the prootic, posterior to the ventral otic fissure and immediately behind the groove for the orbital artery. Elsewhere in osteichthyans the first infrapharyngobranchial (=pharyngobranchial) articulates with the braincase posterior to the ventral otic fissure in the actinopterygian *Cosmoptychius* (Schaeffer 1971: fig. 8), and in the rhipidistians *Eusthenopteron* (Jarvik 1954: fig. 1) and *Ectosteorhachis* (Romer 1937: fig. 2). In most actinopterygians the articulation lies anterior to the fissure owing to the presumed posterior migration of the ventral otic fissure (Gardiner 1970; Gardiner & Bartram 1977). Possible exceptions to this are *Polypterus, Polyodon* and *Acipenser*, in which the limits of the fissure are not precisely determinable, and *Australosomus* (Nielsen 1949: 122) in which the articulation straddles the ventral otic fissure. As a result of the rearward growth of the parasphenoid in *Polypterus*, later palaeoniscids and higher actinopterygians (Gardiner 1973: 115) the first infrapharyngobranchial has often become secondarily associated with it. Thus the first infrapharyngobranchial articulates with the parasphenoid in *Pteronisculus* (Nielsen 1942: fig. 45), *Polypterus, Acipenser, Amia, Lepisosteus*, Upper Jurassic leptolepids (Patterson 1975: 398) and many other teleosts, whereas in *Polyodon* it articulates in the notch between the ascending and posterior processes of the parasphenoid. In pholidophorids (Patterson 1975: 398), parasemionotids, most caturids (*Caturus*, Patterson 1975: 398; *Heterolepidotus*, Patterson 1975: fig. 102; *'Aspidorhynchus'*, Patterson 1975: fig. 99), pachycormids (*Pachycormus*, Patterson 1975: fig. 106) and semionotids (*Dapedium*, Patterson 1975: fig. 112; *Lepidotes*, Patterson 1975: fig. 108) the situation is as in *Polyodon* except that there is a well-marked facet on the prootic and a notch in the overlying parasphenoid. In all these actinopterygians the articulation remains (as far as can be deduced in the fossil forms) approximately on the level at which the lateral aortae give rise to the orbital arteries. Primitively then in osteichthyans the first infrapharyngobranchial articulated with the prootic behind the ventral otic fissure and orbital artery.

The pharyngobranchials of acanthodians are homologous with those of selachians and with osteichthyan supra+ infrapharyngobranchial (see p. 362). The pharyngobranchials of selachians and acanthodians project posteromedially (Nelson 1968; Miles 1973*a*: 96; Jarvik 1977: fig. 8) and this is primitive for gnathostomes. Pharyngobranchials in chondrichthyans and placoderms are usually located posterior to the neurocranium, but in *Heterodontus* and several other sharks as well as holocephalans the first pharyngobranchial lies close to the underside of the occiput though never articulating with it. This latter condition is considered to be derived, as suggested by Miles (1971*a*).

According to Miles (1973*a*: 88) the second pharyngobranchial in *Acanthodes* articulated with the ventral occipital ossification by a facet just behind a groove for an efferent branchial artery. This would be impossible if the pharyngobranchial were backwardly projecting; I suggest the facet may have served for the articulation of the first epibranchial.

The change in branchial arch suspension in osteichthyans, with the development of the forwardly-directed first infrapharyngobranchial (articulating with the braincase) and the development of the suspensory first suprapharyngobranchial, is presumed to be related to the increasing importance of the levator arcus palatini muscles and to the hyoid bar pump in expanding the orobranchial chamber.

4. *Lateral commissure and trigeminofacialis chamber*. The lateral commissure is penetrated by the jugular canal and forms the side-wall to the trigeminofacialis chamber in osteichthyans. It was first described in actinopterygians (*Amia, Lepisosteus, Salmo*), where it is formed (de Beer 1926: 332; 1937: 391) by the junction of the prootic process (developed from the otic capsule) with the basitrabecular and postpalatine processes (developed from the edge of the basal plate).

There has been much discussion as to whether the lateral commissure has a neurocranial or visceral origin. In actinopterygians there is little doubt that the commissure is entirely neurocranial in origin according to the work of Swinnerton (1902) on *Gasterosteus*, de Beer (1926, 1937) on *Amia* and *Salmo*, Hammarberg (1937) on *Lepisosteus*, Hubendick (1943) on *Leuciscus*, Daget & d'Aubenton (1957) on *Heterotis* and Bertmar (1959) on *Hepsetus*. Only Holmgren (1943: 33, 37, 42) suggested that the lateral commissure in actinopterygians is a visceral structure, because in *Acipenser, Amia* and *Lepisosteus* he found a membranous basal connection between the palatoquadrate and trabecular region, which he homologized with the spiracular cartilages in sharks. Since there is no suggestion of a transfer of cartilage from the palatoquadrate (or any other visceral source) to the neurocranium Holmgren's assumptions seem ill-founded. Bertmar (1959: 339) reinvestigated Holmgren's (1943) material and concluded that the lateral commissure in *Acipenser, Amia* and *Lepisosteus* is a primary neurocranial structure, as de Beer (1926: 332) had originally said.

The initial suggestion that the lateral commissure was of visceral origin was made by Allis (1914*a*), who maintained that in *Neoceratodus* it came from the mandibular arch. Holmgren (1940; 1943: 43) later claimed to have furnished complete evidence that the lateral commissure in sharks was derived from the mandibular arch. This evidence consists of a membranous connection between the postorbital process and the basiotic lamina in embryo *Squalus* (Holmgren 1940: fig. 67), a membranous connection between the same process and the hyomandibula in *Etmopterus* (Holmgren 1940: figs 81, 89) and between the postorbital process and the spiracular cartilages in *Raja* (Holmgren 1940: 184). In none of Holmgren's descriptions is there any indication of chondrification within this membrane, other than the formation of spiracular cartilages ventrally. Jollie (1971: 37) confirmed the mandibular arch origin of the lateral commissure in *Squalus*, even though he regarded the structure as a mandibular commissure, not as the lateral commissure proper, which he equated with part of the otic capsule unrelated to the jugular vein. Bertmar (1959: 314, 339) pointed out that while Allis's (1914*a*) deductions were founded on imperfect information in *Neoceratodus*, Holmgren (1940, 1943) had confused the lateral commissure of sharks with mandibular arch structures (see also Bjerring 1967: 262). However, Bertmar (1959: 314; 1963: 337) went on to suggest that the lateral commissure in *Neoceratodus* is derived from the hyoid arch and represents fused infra- and suprapharyngohyals, and thus added some credence to the theory of the hyal origin of the commissure in *Eusthenopteron* proposed by Jarvik (1954: 75).

The only possible confirmation of Bertmar's (1959) theory would be to show that the lateral commissure in selachians is of hyoid arch origin, which is exactly what Jollie (1971: 37) proposed. Unfortunately, Jollie homologized the lateral commissure of actinopterygians with the otical shelf of sharks, despite the fact that a lateral commissure exists in many selachians (*Oxynotus, Scymnodon, Centrophorus, Cladodus*; Holmgren 1940, 1941) and is massive in *Squatina* and many fossil sharks (*Xenacanthus, Tamiobatis, Hybodus*). Thus from the evidence presented by Holmgren (1940), El-Toubi (1949) and Jollie (1971) for *Squalus*, and Holmgren (1940) for *Etmopterus*, there is no reason to suppose that the lateral commissure in selachians forms in a manner significantly different from that in actinopterygians. Furthermore, although the lateral commissure is missing in hexanchoids, galeomorphs, many rays, torpedoes and chimaeroids, its presence in other selachians, osteichthyans, placoderms (Young 1980) and acanthodians (Miles 1973*a*: fig. 4) suggests it is a primitive feature of gnathostomes.

Allis (1914*b*, 1919) first introduced the term 'trigeminofacialis chamber' for the space in the side wall of the braincase of actinopterygians immediately in front of the auditory capsule. This chamber is made up by the pars ganglionaris and the pars jugularis. Allis pointed out that the trigeminofacial chamber is single in *Amia* and *Lepisosteus* because the pars ganglionaris and pars jugularis are confluent, but that in *Scomber* and the scorpaenoid teleosts the chamber is divided. Goodrich (1930: 277), knowing that in selachians the trigeminal and facial ganglia are intramural, decided that the condition in *Amia* and *Lepisosteus*, in which an intramural recess (pars ganglionaris) is confluent with an extramural recess (pars jugularis), represents the basic configuration for actinopterygians. He further believed that in teleosts the trigeminofacial chamber is secondarily divided by a bony wall. This view was also held by de Beer (1937: 56, 428), who qualified it by pointing out that the trigeminofacial chamber of *Amia* could be derived from the condition in *Squalus* if the acustico-trigeminofacialis recess and the jugular canal of the latter 'were thrown into one'. Earlier (de Beer 1926), however, he had shown that the trigeminofacial chamber is separate from the jugular canal in the development of *Acipenser* and *Amia*.

In chondrichthyans the pars jugularis is separated from the pars ganglionaris by the lateral wall of the neurocranium (prefacial commissure), whereas the medial wall of the trigeminofacialis chamber (prefacial commissure + pila antotica) is invariably complete and ossified in palaeoniscids, fossil halecostomes, halecomorphs and all the major groups of teleosts. From this it is clear that the condition in *Amia, Lepisosteus* and certain advanced teleosts in which the prefacial commissure and pila antotica fail to ossify, thereby allowing the chamber to communicate widely with the cranial cavity, is specialized.

Unlike chondrichthyans the facial and trigeminal ganglia are primitively extracranial in actinopterygians. This is certainly the case in palaeoniscids, *Polypterus, Acipenser,* caturids, *Lepidotes*, pholidophorids and early leptolepids, whereas in *Ichthyokentema*, Upper Jurassic leptolepids and primitive living teleosts the geniculate and gasserian ganglia are partly or wholly intracranial (Patterson 1975: 401). Schaeffer (1971: 7) attempted to reconcile the varying locations of the two ganglia in the jugular canal of different actinopterygian groups, by suggesting that the term 'trigeminofacialis chamber' be restricted to the extramural cavity between the lateral cranial wall and the lateral commissure. If we accept this simple definition then it is obvious that the trigeminofacialis chamber of primitive actinopterygians (palaeoniscids, *Polypterus, Acipenser*, etc.) is not very different from that of selachians such as *Oxynotus, Squatina* and *Squalus*. Since such a chamber is also found in placoderms (*Brindabellaspis*, Young 1980: fig. 10) it must be considered a primitive gnathostome character. Nevertheless, because the geniculate and gasserian ganglia have varied relationships to this extramural cavity (trigeminofacialis chamber) and to the mouth of the jugular canal in actinopterygians and selachians, it is necessary to establish the primitive condition in actinopterygians, osteichthyans and gnathostomes.

(a) ACTINOPTERYGIANS. In most palaeoniscids the lateral commissure is a massive endochondral structure formed by the prootic and penetrated by a long jugular canal. The commissure is also massive in *Polyodon* but is less extensive in *Polypterus, Acipenser, Mimia* and *Moythomasia* and is considerably reduced in *Amia, Lepisosteus*, parasemionotids, caturids, semionotids, pachycormids and pholidophorids. The lateral wall of the jugular canal in many palaeoniscids is perforated by several other canals; a ventral one which transmitted the orbital artery, and one or more dorsal foramina which transmitted the hyomandibular trunk or its branches, or both. Actinopterygians with three separate posterior openings (for the jugular vein, orbital artery and hyomandibular trunk) include *Pteronisculus, Kentuckia, Kansasiella, Perleidus*, leptolepids and other primitive teleosts. Patterson (1975: 400), however, has demonstrated that the condition in teleosts is secondary and developed as a result of extensive membrane bone outgrowths.

The jugular canal may open posteriorly by a single foramen transmitting the jugular vein, orbital artery and hyomandibular trunk as in *Mimia, Acipenser*, parasemionotids, caturids, pachycormids, *Lepidotes, Lepisosteus, Dapedium* and pholidophorids; or the orbital artery may enter by a separate vertical canal as in *Kansasiella, Moythomasia, Boreosomus, Australosomus, Pteronisculus cicatrosus, Saurichthys, Polyodon* and *Amia*; or the orbital artery may pass outside the commissure as in *Polypterus*.

The facial canal, which primitively transmitted only the palatine and hyomandibular trunk of the facial nerve, opens into the ventromedial corner of the orbital opening of the jugular canal in *Pteronisculus, Mimia, Moythomasia, Kentuckia, Boreosomus, Saurichthys, Perleidus* and parasemionotids and the geniculate ganglion lay in the floor of the jugular canal. In *Acipenser* the facial canal emerges in the orbit and the hyomandibular trunk turns posteriorly to traverse the jugular canal.

In *Polypterus* and *Kansasiella* the facial canal opens into the middle of the jugular canal and the geniculate ganglion lay within the jugular canal.

In caturids, *Lepidotes*, pachycormids and pholidophorids, where the lateral commissure is reduced, the facial canal opens just behind the jugular canal.

The lateralis branches of the facial nerve issue through the trigeminal foramen in palaeoniscids, pholidophorids, pachycormids, leptolepids and other teleosts, and in most of these fishes the external opening of the trigeminal canal lies anterodorsal to the facial foramen, in the upper part of the orbital opening of the jugular canal. In *Polypterus* there is a separate lateralis ganglion (lateralis – communis of Allis 1922: 274) dorsal to the trigeminal ganglion. This lateralis ganglion is partly extracranial and partly intracranial and is continuous with the intracranial portion of the facialis ganglion. In *Amia* a similar lateralis ganglion lies above the gasserian ganglion. In *Polyodon* and *Acipenser* the lateralis branches of the facial nerve emerge into the orbit through separate foramina (superficial ophthalmic and otic branches). This is considered to be a specialization following loss of the prefacial commissure in *Acipenser*. Both caturids and *Amia* have an intramural canal for the superficial ophthalmic nerves, and in *Ospia* and some parasemionotids the trigeminal canal is divided by a horizontal partition, with the superficial ophthalmic nerves passing out separately through the dorsal part (Patterson 1975: 405).

In the Gogo palaeoniscids there is a separate foramen dorsal to the facial canal and posterolateral to the trigeminal canal. Although no such foramen or canal has been reported in any other actinopterygian, by comparison with *Polypterus* and *Amia* this foramen must have transmitted the lateralis branches of the facial nerve.

The facial and trigeminal canals originate in front of the recess for the utriculus in *Mimia, Moythomasia, Pteronisculus, Australosomus*, and pholidophorids, but in *Mimia* a bridge of bone separates the facial canal from the lateralis canal and the latter originates in the most anterior part of the utricular recess. In many other palaeoniscids such as *Kansasiella, Kentuckia* and *Boreosomus*, and in *Perleidus* and fossil and living neopterygians (parasemionotids, *Caturus, Lepidotes, Dapedium, Amia, Lepisosteus*), the facial and trigeminal canals originate in the utricular recess. This is considered a specialization (Patterson 1975: 408).

In *Mimia* and all previously described palaeoniscids, chondrosteans, perleidids and pholidopleurids (*Pteronisculus, Kentuckia, Kansasiella, Acipenser, Polyodon, Boreosomus, Birgeria, Perleidus, Australosomus*) the facial canal opens into the orbital opening of the jugular canal (but see Lehman 1969), the geniculate ganglion lay in the floor of the canal, the palatine nerve passed down into the parabasal canal along the hind wall of the orbit, and there is no prefacial (prepalatine) floor to the jugular canal. This is also the condition in parasemionotids, *Lepisosteus* and *Amia* except that in some of the more fully ossified specimens of parasemionotids (Patterson 1975: 405) there are rudiments of a prepalatine strut.

In *Moythomasia*, however, the external opening of the facial canal is confluent with a palatine fenestra, a rather large opening in the floor of the jugular canal. Thus *Moythomasia* is the only palaeoniscid so far described with a prefacial floor to the jugular canal. This prefacial floor has the same proportions as in *Pholidophorus* and *Pachycormus* (Patterson 1975: 404; fig. 64) and the geniculate ganglion must have lain within the palatine fenestra. In *Lepidotes, Dapedium, Leptolepis* and many living teleosts the opening in the floor of the jugular canal decreases in size so that only a palatine foramen remains. The palatine nerve passed through this opening into the myodome and the geniculate ganglion must have lain in the extramural space in the floor of the jugular groove.

In most caturids (*Heterolepidotus, 'Aspidorhynchus', Caturus, Macrepistius*) the prepalatine floor is represented by a slender strut, but in the *Caturus* described by Rayner (1948: fig. 5) the floor is more complete and similar to that in *Moythomasia* and *Pholidophorus*.

The otic nerve canal originates in the wall of the orbit above the opening of the jugular canal in

Mimia, Moythomasia, Kansasiella, Perleidus, Polypterus, parasemionotids, *Dapedium, Lepidotes, Pachycormus* and *Pholidophorus*, but in *Pteronisculus, Kentuckia, Boreosomus, Australosomus, Heterolepidotus, Caturus, Macrepistius, Amia* and *Lepisosteus* it originates in the roof of the mouth of the canal. The otic nerve canal passes through the postorbital process to join the spiracular canal in *Boreosomus, Australosomus, Lepidotes, Pachycormus*, and *Pholidophorus*, while in *Kansasiella* (Poplin 1974: fig. 12) it is only just excluded from the top of the spiracular canal. But in *Pteronisculus, Kentuckia, Saurichthys, Acipenser*, parasemionotids, *Dapedium, Heterolepidotus, Lepisosteus* and *Amia* the otic canal opens into the floor of the fossa bridgei, medial to the spiracular canal. In larval *Amia* (Goodrich 1930: fig. 733) the otic nerve passes into the top half of the spiracular canal and not into the fossa bridgei, and in *Polypterus* the otic nerve perforates the postorbital process, passes beneath the ampulla of the anterior semicircular canal and emerges on the roof of the neurocranium medial to the most anterior portion of the spiracle. In *Mimia* and *Moythomasia* the otic nerve canal similarly passes through the postorbital process medial to the spiracular groove.

The superficial ophthalmic nerves are believed to have emerged through the trigeminal foramen in palaeoniscids, *Perleidus, Dapedium, Lepidotes, Pachycormus* and *Pholidophorus*. In *Moythomasia* there is a short canal leading upwards from the roof of the recess for the trigeminal and lateralis ganglia. This canal passes up through the wall of the orbit (pterosphenoid pedicel) and must have served for the superficial ophthalmic nerves. Loss of the separate lateralis canal and enlargement of the external opening of the trigeminal canal would lead to the condition seen in *Kentuckia, Ospia*, caturids and *Amia*.

There is a separate profundus foramen in *Mimia, Moythomasia, Kentuckia, Kansasiella, Pteronisculus, Perleidus*, parasemionotids, caturids, *Lepidotus, Lepisosteus, Dapedium, Pachycormus*, pholidophorids and the Sinemurian *Leptolepis*, but in all other leptolepids there is no separate profundus foramen. In some living teleosts there is a separate profundus foramen, but in many others the nerve enters the orbit through the oculomotor foramen, as in *Polypterus*. There is no sign of a profundus foramen in *Boreosomus, Saurichthys* or *Australosomus* and there is no separate foramen in *Amia*. From this evidence it is not clear whether a separate profundus foramen is primitive. In *Mimia* the root of the profundus, together with the trigeminal nerve, passed into the base of the trigeminal canal. The trigeminal canal immediately divides and the profundus passed forwards and downwards to enter the orbit through a separate foramen. The condition in *Boreosomus, Saurichthys* and *Australosomus* could be derived from that in *Mimia* merely by enlargement of the trigeminal canal, so that the profundus emerged with the trigeminal nerve (see also Nielsen 1949: 58), as in selachians.

From this survey I conclude (as did Patterson 1975: 408) that primitively in actinopterygians the lateral commissure was massive and that the posterior lateral wall of the jugular canal was perforated by the hyomandibular trunk dorsally and the orbital artery ventrally. The extracranial gasserian and geniculate ganglia lay in the mouth of the orbital opening of the jugular canal and the facial and trigeminal canals originated in front of the utricular recess. The facial canal transmitted the palatine nerve and hyomandibular trunk, with the latter turning posteriorly to traverse the jugular canal and with the palatine nerve passing into the parabasal canal. The trigeminal canal opened into the orbit dorsomedial to the facial canal and the otic nerve canal originated in the wall of the orbit above the jugular canal and passed up onto the roof of the neurocranium medial to the spiracle.

(b) OSTEICHTHYANS. In actinistians the lateral commissure is well developed (*Nesides*, Bjerring 1977: fig. 23a; *Macropoma, Latimeria*, Millot & Anthony 1958) and is similar to that in the Gogo palaeoniscids. The jugular canal is long and transmits the hyomandibular trunk, orbital artery and jugular vein in *Latimeria*. In rhipidistians such as *Eusthenopteron* (Jarvik 1954: fig. 1), *Ectosteorhachis* (Romer 1937: fig. 2), *Porolepis* (Bjerring 1967: 224) and *Glyptolepis* (Jarvik 1972: fig. 21) the lateral commissure is also massive and the jugular canal is similar in length to that in palaeoniscids and actinistians. The lateral commissure is not easily recognizable in adult dipnoans owing to fusion of that region with the palatoquadrate, but Bertmar (1963: 337) believed it can readily be distinguished in embryos of *Neoceratodus*. A long jugular canal is present and transmits the hyomandibular trunk, jugular vein and orbital artery, as in many actinopterygians. In the Devonian dipnoans *Griphognathus* and *Holodipterus* there are separate posterior openings (Miles 1977: figs 14, 44) for these three structures, as in primitive actinopterygians, but in *Chirodipterus* there are two, one for the jugular canal and the other for the hyomandibular trunk and the orbital artery, while in the Recent *Neoceratodus* there is a single posterior opening for all three structures.

In some actinistians (*Nesides, Latimeria*) the opening of the facial canal lies in front of the jugular canal, but in *Rhabdoderma* and the rhipidistians *Ectosteorhachis, Eusthenopteron, Glyptolepis* (Jarvik 1972: fig. 21) and *Youngolepis* (Chang 1982: 51) the facial canal opens into the mouth of the jugular canal much as in palaeoniscids.

In the Devonian dipnoan *Griphognathus* (Miles 1977: fig. 53) the root of the facial nerve opens into the centre of the jugular canal, but the anterior part of the jugular canal is considered a dipnoan specialization, formed by fusion of the ascending process of the palate to the pila antotica. The facial and trigeminal ganglia were extracranial as in *Neoceratodus*.

In *Latimeria* (Millot & Anthony 1958) the gasserian and geniculate ganglia are separate and intramural, the geniculate ganglion lies between the two moieties of the braincase, and there is no separate lateralis canal. In fossil actinistians such as *Diplocercides* they may also be assumed to have been intracranial.

In rhipidistians such as *Ectosteorhachis* (Romer 1937: fig. 2) and *Eusthenopteron* (Jarvik 1954: fig. 1A; Bjerring 1971: fig. 9) the facial and trigeminal ganglia appear to have been intracranial.

The trigeminal, facial and lateralis canals arise in front of the recess for the utriculus in the dipnoans *Griphognathus* and *Chirodipterus* (Miles 1977: figs 10, 17) and all the branches of the trigeminal and facial nerves appear to originate well in front of the utricular recess in *Eusthenopteron* (Jarvik 1975: fig. 14) and *Ectosteorhachis* (Romer 1937: figs 8, 13). The otic canal originates above the jugular canal in the actinistians *Latimeria, Nesides, Rhabdoderma* and *Laugia* and the rhipidistians *Eusthenopteron, Ectosteorhachis, Rhizodopsis* and *Glyptolepis*. The otic nerve canal originates behind the spiracular groove in *Eusthenopteron* (Jarvik 1954: fig. 1, spic) and opens into the anterior portion of the post-temporal fossa. In *Youngolepis* (Chang 1982: fig. 15A, r.ot.l) the otic nerve ran in a groove (anterodorsal to the lateral commissure) which terminates below the temporal sensory canal. In *Latimeria* the otic nerve passes up behind the spiracle.

A separate canal for the superficial ophthalmic nerves is found in *Griphognathus* (Miles 1977: figs 10, 33, 55, VIIs?) and *Chirodipterus* (Miles 1977: figs 21, 35, 38, VI?). In *Diplocercides* (Bjerring 1971; 1977: fig. 23A) a somewhat smaller foramen above the facial canal must have also served for the lateralis branches of the facial nerve. The lateralis root in *Latimeria* exits through the intracranial joint.

There is a separate profundus canal in actinistians and Devonian dipnoans. In actinistians (*Latimeria, Rhabdoderma, Macropoma, Nesides*) it is within the 'basisphenoid', but in *Chirodipterus* (Miles 1977: figs 17, 47) its origin is just in front of the trigeminal canal and above the prootic bridge (as in palaeoniscids).

Thus from this brief summary I conclude that the osteichthyan morphotype must have been similar to the actinopterygian one outlined above, apart from the path of the otic nerve canal.

(c) GNATHOSTOMES. In primitive sharks such as *Hybodus* (BMNH P.50869, Maisey 1983) and *Xenacanthus* (Schaeffer 1981: fig. 6) the lateral commissure is a massive structure of calcified cartilage penetrated by a long jugular canal much as in *Polyodon*, but only the jugular vein and hyomandibular trunk passed through it. In *Xenacanthus, Cladodus* and *Squalus*, the hyomandibular trunk exits through a separate foramen. In many other selachians such as *Scymnodon* and *Oxynotus* the hyomandibular trunk exits from the skull posterior to the jugular canal and does not pass through it; this is considered specialized and related to the posterior position of the hyomandibula. A lateral commissure is also clearly recognizable in pristiophorids, some rhinobatoids (Compagno 1977: 310, 316) and *Squatina* (Holmgren 1941: 36). The orbital artery never passes through the jugular canal or the lateral commissure; instead it often pierces the subotical shelf (cf. *Squalus*). The palatine nerve, on the other hand, may pierce the basal part of the lateral commissure (*Tamiobatis, Xenacanthus, Squalus*).

The facial canal is variable in position in selachians. In *Scymnorhinus* the facial canal opens into the middle of the jugular canal as in *Polypterus* (except that the ganglion is intramural), but in *Rhinobatus*, where the lateral commissure is reduced, the facial canal opens in front of the jugular canal and in *Etmopterus* and *Squatina* it opens into the ventromedial corner of the orbital opening of the jugular canal, as in many palaeoniscids and parasemionotids.

In most selachians the lateralis branches of the facial nerve issue through the trigeminal foramen, as in actinopterygians, and the trigeminal foramen often lies in the orbital opening of the jugular canal (*Oxynotus, Scymnodon, Xenacanthus, Tamiobatis, Cladodus, Hybodus*). In other selachians (*Etmopterus, Squatina, Rhinobatus*) the trigeminal foramen opens in front of the jugular canal. The gasserian and geniculate ganglia are always intracranial. The otic nerve canal passes from the orbit up through the postorbital process to open on the roof of the neurocranium medial to the spiracle in *Chlamydoselachus* and *Heterodontus*, and there is a separate foramen for the profundus.

A massive lateral commissure is also found in Devonian placoderms such as *Brindabellaspis* and *Buchanosteus* (Young 1979; 1980: figs 8, 9) and the jugular canal is longer proportionally than in primitive actinopterygians. The hyomandibular trunk passed out through the anterior opening of the jugular canal in *Brindabellaspis*, but passed across the canal (at right angles to it) in *Buchanosteus*. The orbital artery entered the jugular canal by a separate foramen in *Kujdanowiaspis* (Young 1979: 329), but in *Buchanosteus* (Young 1979: fig. 9) it passed lateral to the jugular canal and in *Brindabellaspis* (Young 1980: 41) medial to it.

The facial canal seems to be less variable in position in placoderms than selachians. In *Brindabellaspis* and *Wijdeaspis* (Young 1978, 1980) it opens into the mouth of the jugular canal, but in *Buchanosteus* (Young 1979) the facial canal opens into the anterior half of the jugular canal. There is a separate profundus canal in *Jagorina, Brindabellaspis* and *Macropetalichthys* and a separate canal for the superficial ophthalmic nerves in *Buchanosteus* (Young 1979: fig. 5).

In *Acanthodes* the lateral commissure is not really discernible because of lack of ossification in that region, but a short perichondral commissure is present as Miles (1973*a*: fig. 4) presumed (BMNH specimens).

From this brief survey I conclude that the primitive gnathostome possessed a long lateral commissure with separate openings for the jugular vein and hyomandibular trunk; the facial canal emerged in the orbital opening of the jugular canal and the trigeminal canal dorsomedial to it; the otic nerve canal originated in the posterior wall of the orbit and passed up to the neurocranial roof medial to the spiracle.

5. *Hyomandibular facet.* In the Gogo palaeoniscids this lies obliquely between the sphenotic and opisthotic with the prootic forming a small portion of the ventral margin. A similar oblique facet above the jugular canal is characteristic of most palaeoniscids, *Polyodon, Acipenser, Polypterus*, etc.

In later actinopterygians such as amioids, semionotids, pachycormids, pholidophorids and Recent teleosts the facet has become more or less horizontal. In amioids, pholidophorids and pachycormids it lies between the sphenotic and prootic anteriorly and the pterotic and opisthotic posteriorly (except in *Amia* and semionotids), while in leptolepids and many other teleosts the posterior end lies entirely within the pterotic. There is a single hyomandibular articulation in actinopterygians and the oblique facet in palaeoniscids is considered primitive.

In actinistians the hyomandibular articulation is a very large, bilobed, cartilage-capped area (*Nesides*, Bjerring 1977: fig. 23; *Rhabdoderma*, Forey 1981: fig. 1; *Latimeria*, Millot & Anthony 1958) which straddles the jugular canal obliquely and lies between the prootic and opisthotic. In rhipidistians (*Eusthenopteron*, Jarvik 1954: fig. 1; *Ectosteorhachis*, Romer 1937: fig. 2; *Porolepis*, Bjerring 1967: 224; *Youngolepis*, Chang 1982: fig. 15A) the articulation is double, oblique and crosses the jugular canal. I assume it lies between the prootic and opisthotic in *Eusthenopteron*. The hyomandibular facet in Devonian dipnoans straddles the jugular canal obliquely, as in actinistians and rhipidistians (Miles 1977: 90), and the articulation is divided into dorsal and ventral areas by a thin tract of perichondral bone. Despite the arguments of Miles (1977: 91) I see no reason to change my previous view (Gardiner 1973: 109, 122) that the hyomandibula has a double articulation with the neurocranium in Devonian dipnoans, much as in rhipidistians. In Recent dipnoans the facet is lost.

In *Acanthodes* (Miles 1964: fig. 1B) the head of the hyomandibula is presumed to have lain obliquely between the perichondral lateral commissure and otic ossification and dorsal to the jugular canal, as in actinopterygians.

In chondrichthyans the condition is variable. In *Heptanchus, Squatina* (Holmgren 1941: 30) and *Cobelodus* (Zangerl & Case 1976) the hyomandibular facet is set obliquely across the posterior part of the auditory region and in *Mustelus, Carcharinus* and *Heterodontus* (Holmgren 1941: 45) the articulation is on the anterior half of the auditory region. In *Chlamydoselachus* and *Orectolobus* the hyomandibular facet is a long, broad groove dorsal to the auditory bulla, whereas in *Squalus* it is below and behind the bulla. In *Rhinobatus, Raja, Discobatus, Pristis, Pristiophorus, Dasybatus* (Holmgren 1941) and all other rays the articulation is divided into two facets which are situated in the posterior part of the auditory region. In all these Recent sharks and rays without exception the hyomandibula articulates with the endocranium ventral to the jugular vein, and usually below the ridge for the horizontal semicircular canal, and is suspensory. This ventral position of the hyomandibula with respect to the jugular vein in selachians has generated much argument as to whether the condition is primitive (Holmgren 1943: 102, 104) or advanced (Gardiner 1973: 122), while its posterior position has been responsible for the development of elaborate theories of the incorporation of hyoid arch material (pharyngohyal) into the auditory capsule (Holmgren 1940; 1943: 43, 68), to form the otical shelf and hyomandibular facet in rays. Jarvik (1954: 75) has used this supposed evidence of incorporation of the hyoid arch material into the auditory capsule of selachians to support a similar presumed incorporation of hyoid arch material into the lateral commissure and 'otical shelf' region of *Eusthenopteron*. However, the supposed incorporation of hyoid material in sharks and rays described by Holmgren (1940, 1943) always occurs posterior to the lateral commissure (Holmgren 1940: fig. 130), whereas the 'otical shelf' of *Eusthenopteron* (Jarvik 1954: fig. 1A) lies anterior to the lateral commissure. But the discovery in *Tristychius* (Dick 1978) and *Hybodus* (Maisey 1982, 1983) of a hyomandibula which articulated with the braincase above the jugular canal as in actinopterygians, actinistians and rhipidistians suggests that it is no longer worth while to invoke theories of hyoid arch incorporation to explain the 'otical shelf' in selachians.

In those placoderms in which the hyomandibular articulation has been described in detail (Young 1980, Stensiö 1963*a*, Goujet 1975) it is at the base of the lateral commissure (*Brindabellaspis* Young 1980) and in front of the foramen for the hyomandibular trunk.

I conclude that primitively in gnathostomes the hyomandibula must have articulated with the braincase in the region of the lateral commissure and was suspensory. Whether the articulatory facet is above or below the jugular canal seems of little significance and there is no reason to suppose that the hyomandibular–neurocranial attachment developed more than once.

6. *Otico-sphenoid fissure*. This has so far only been reported in the Gogo palaeoniscids. It was cartilage-filled and separates the anteroventral corner of the prootic from the basisphenoid. It appears to correspond with the gap between the lateral commissure and the polar cartilage – trabecular bar of the embryo actinopterygian (Gardiner & Bartram 1977: 241). Together with the ventral otic fissure it is homologous with the ventral part of the intracranial joint of actinistians and rhipidistians (Gardiner & Bartram 1977: 242). However, this homology has been denied by Bjerring (1978).

7. *Fossa bridgei and lateral cranial canal*. The Gogo palaeoniscids resemble *Boreosomus* (Nielsen 1942) in the considerable variation shown in the degree of ossification of the dorsal otic region. In some specimens of *Mimia* (Fig. 12) there is large lateral cranial canal in the roof of the otic region occupying the whole of the area between the posterior and anterior semicircular

canals. This chamber is roofed by a sutureless skin of perichondral bone and connects with the cranial cavity posteriorly by a large opening through the loop of the posterior semicircular canal (Fig. 26). Anteriorly it may occasionally connect with the cranial cavity in front of the sinus superior by various small foramina. The supratemporal branch of the glossopharyngeal nerve enters the canal laterally. The spiracular groove lies anterolateral to the canal and is not included within it. In other specimens of *Mimia*, the lateral cranial canal is little more than a pocket in front of the posterior semicircular canal, but still maintains its posterior connection with the cranial cavity by a large foramen through the loop of the semicircular canal much as in *Kansasiella* (Poplin 1974: fig. 20, e.l.m, y) and *Kentuckia* (Rayner 1951: fig. 9, x).

The presence of a lateral cranial canal is considered to be a specialization of actinopterygians (Gardiner 1973: 113). Jarvik (1980) has shown that in Recent chondrosteans and holosteans there is a hemopoietic organ dorsal to the medulla which in *Lepisosteus* has earlike lobes passing forwards and upwards into the lateral cranial canal.

The Gogo palaeoniscids have no fossa bridgei, which if present would have overlain (in part) the lateral cranial canal. A lateral cranial canal is well developed in *Kentuckia* but the fossa bridgei is poorly defined and consists of several irregular cavities (Rayner 1951: figs 6, 9). Most palaeoniscids possess both a lateral cranial canal and a fossa bridgei, but the absence of the latter in the Gogo palaeoniscids is considered primitive.

In *Polypterus* there is neither a fossa bridgei nor a lateral cranial canal and this is considered primitive for osteichthyans. Actinopterygians in which the fossa bridgei and lateral cranial canal are separate include *Kansasiella, Boreosomus, Pholidophorus* (Patterson 1975: 336), *Leptolepis* (Patterson 1975: fig. 73), *Caturus* (Rayner 1948: fig. 9), *Heterolepidotus, Dapedium, Lepidotes*, parasemionotids and *Lepisosteus* (Gardiner 1973: 13). In many other actinopterygians there is a connection between the deeper, posterior part of the fossa bridgei and the cranial cavity (Nielsen 1942: 294; Patterson 1975: 392, 414). These connections are topographic homologues of parts of the lateral cranial canal. Forms in which the fossa bridgei communicates posteriorly with the cranial cavity by way of the lateral cranial canal include *Pteronisculus*, some specimens of *Boreosomus*, and *Polyodon* (cf. *Boreosomus* Nielsen 1942: fig. 59, where in one individual the fossa bridgei is separated by bone from the lateral cranial canal on one side, but on the other the two cavities are connected).

In several other actinopterygians (*Ospia, Acipenser*) where the lateral cranial canal and fossa bridgei have become confluent the lateral cranial canal portion has lost its connection with the cranial cavity; this is also considered to be a specialization. The lateral cranial canal communicates with the cranial cavity posteriorly through the loop of the posterior semicircular canal in the Gogo palaeoniscids, *Kansasiella* (Poplin 1974: fig. 22), *Kentuckia, Boreosomus* and *Polyodon*, but in caturids (*Caturus, Heterolepidotus*) and pholidophorids the canal has both anterior and posterior openings into the cranial cavity and in *Perleidus* there is only an anterior opening (Patterson 1975: 414). In leptolepids, *Lepisosteus* and *Lepidotes* the lateral cranial canal has lost the inner wall and thus has the form of a posterodorsal diverticulum of the cranial cavity (Patterson 1975: 413). In *Polyodon* the connection between the fossa bridgei and the cranial cavity, by way of the lateral cranial canal, is fat-filled.

The spiracular groove in the Gogo palaeoniscids and the spiracular canal in *Kentuckia* lie lateral to the area occupied by the fossa bridgei in other forms, and in *Polypterus* the spiracle lies alongside the braincase in the adult. The spiracle also lies freely alongside the intracranial joint in *Latimeria*. In *Eusthenopteron* Jarvik (1954: fig. 1A, spic) has claimed that a spiracular canal enters the fossa bridgei. However, the 'fossa bridgei' in *Eusthenopteron* is more reasonably interpreted as a post-temporal fossa and the 'spiracular canal' as the otic nerve canal. Subsequent evolution within actinopterygians brought about the formation of the spiracular recess (often called 'fossa bridgei anterior', Nielsen 1942: fig. 11) containing a blind-ending spiracular diverticulum in *Acipenser, Polyodon* and *Amia*. The recess is confluent with the fossa bridgei (Gardiner 1973: 114) in these fishes. In the Gogo palaeoniscids the spiracular groove is entirely outside the sphenotic, but in halecomorphs and pholidophorids the spiracular canal penetrates the postorbital process at the junction between the sphenotic and prootic (Patterson 1975: 399). The condition in which the fossa bridgei includes the spiracular recess but is still roofed by dermal bone is met with in *Polyodon, Boreosomus, Perleidus, Acipenser, Ospia,* parasemionotids, caturids and pholidophorids.

In *Amia* and *Lepisosteus* the fossa bridgei is represented by an elongate pocket or groove, containing no musculature, which extends anteriorly to the opening of the spiracular canal. An area medial to the anterior semicircular canal in *Pholidophorus*, referred to as the antero-medial portion of the fossa bridgei by Patterson (1975), has no homologue in the Gogo palaeoniscids and is presumably a specialization of later actinopterygians.

In parasemionotids and primitive pholidophorids, behind the fossa bridgei and separated from it by a wall of bone, there is a small post-temporal fossa which probably contained trunk musculature (Patterson 1975: 392). In Upper Jurassic pholidophorids the post-temporal fossa and fossa bridgei have become confluent, by the breakdown of the intervening wall, allowing the axial muscles to extend into the fossa bridgei, as in Recent teleosts (Patterson 1975: 392). There is no homologue of the post-temporal fossa in palaeoniscids, but a rudimentary post-temporal fossa appears to be present in *Birgeria, Perleidus, Saurichthys*, and sturgeons (Griffith & Patterson 1963: 35; Patterson 1975: 392). The post-temporal fossa is presumed to be a specialization of later actinopterygians, and Patterson (1975: 393) has shown how the pre-epiotic pocket of primitive teleosts is the topographic homologue of the posteromedial portion of the fossa bridgei of pholidophorids and primitive leptolepids. A further small blind-ending fossa (wrongly referred to as a pre-epiotic fossa by Gardiner, 1973: 113) which runs down under the posterior semicircular canals in the clupeid *Alosa* (Todd 1973) is possibly the homologue of the lateral cranial canal of *Pholidophorus*.

There is no evidence of a fossa bridgei in *Latimeria* or any fossil actinistian (including *Nesides*). A small post-temporal fossa is present in some later actinistians and receives trunk muscles in *Latimeria*; this must have developed in parallel with that in later actinopterygians and rhipidistians (see below).

A well-developed post-temporal fossa is also present in many rhipidistians, and in *Eusthenopteron* (Jarvik 1954; 1975: figs 8, 9, 11, 13; fossa bridgei) it is roofed by dermal bone. It lies between the posterior and anterior semicircular canals and is limited laterally by the parotic crista which encloses the external semicircular canal. It is in a similar position to the posterior part of the fossa bridgei and the lateral cranial canal in palaeoniscids. Presumably it was invaded by axial muscles much as in later actinopterygians, actinistians and tetrapods. A similar post-temporal fossa is found in *Ectosteorhachis, Rhizodopsis, Osteolepis* and *Glyptolepis*.

In Devonian dipnoans, according to Miles (1977: 74), there is a fossa comparable to that in rhipidistians, the masseter fossa. It is limited laterally by the parotic crista (which encloses the external semicircular canal), roofed by dermal bone, and extends medial to the posterior vertical semicircular canal; the fossa is open posteriorly. However, since the fossa in Devonian dipnoans is presumed to have housed only the adductor mandibulae (cf. *Neoceratodus*) it may not be homologous with the rhipidistian post-temporal fossa as Miles assumed. Moreover, although a post-temporal fossa is present in many amphibians (loxommatids) it is missing in primitive temnospondyls, anthracosaurs and other primitive amniotes.

The fossa bridgei is recognizable only in later actinopterygians and its absence is considered a primitive osteichthyan feature. There is no indication of a fossa bridgei or a post-temporal fossa in acanthodians, placoderms or chondrichthyans.

8. *Spiracle and spiracular canal.* In the Gogo palaeoniscids the spiracular groove is long and the spiracle was open. However, in some specimens of *Moythomasia* the groove is embraced dorsally by a thin ring of bone (Fig. 83) similar to that described in *Eusthenopteron* (Jarvik 1954: fig. 1B, b.al). The spiracle opened dorsally through a slit in the dermal roof. In *Polypterus* the anterior edge of the spiracular pouch lies in the fossa spiracularis (Allis 1922: 193) and the spiracle opens through a slit between the 'parietal' and two spiracular ossicles.

In *Acipenser, Polyodon* and *Lepisosteus* the spiracular pouch divides into two tubes, one of which opens on the skull roof (spiracle) and the other forms the blind-ending spiracular canal. In *Amia* only the blind-ending spiracular canal remains. A homologous spiracular canal penetrates the postorbital process of most palaeoniscids and other primitive actinopterygians. The spiracular canal is still relatively short in *Pteronisculus, Kansasiella* and *Kentuckia* and is presumed to be contained within the sphenotic. The canal is proportionally longer in *Boreosomus, Birgeria, Perleidus, Australosomus, Acipenser* and *Polyodon*, but in these last two living chondrosteans it is housed in cartilage.

A spiracular canal (or dorsal diverticulum) is found in many selachians where it is contained within the ventrolateral wall of the auditory capsule, below the external semicircular canal. Another more ventromedial diverticulum houses a spiracular sense organ. This dorsal or auditory diverticulum of sharks is directed towards the ventral wall of the auditory 'capsule' whereas that of *Acipenser, Lepisosteus* and *Amia* passes up along side the trigeminofacialis chamber before piercing the postorbital process. From this evidence and from the fact that in *Latimeria* the spiracle was also unenclosed and without a diverticulum, the condition in the Gogo palaeoniscids, *Polypterus* and *Latimeria* is considered primitive for osteichthyans. Subsequent evolution within the actinopterygians led towards elongation of the enclosed portion of the spiracular canal at the expense of the spiracular groove (Patterson 1975: 399) and the spiracular canal came to open within the fossa bridgei (Gardiner 1973: 113). A long spiracular canal is found in parasemionotids, caturids (*Caturus*, Rayner 1948: fig. 5; *Heterolepidotus*, Patterson 1975: fig. 102; *'Aspidorphynchus'*, Patterson 1975: fig. 99), amiids (*Sinamia*, Stensiö 1935; *Enneles*, Santos 1960), semionotids (*Dapedium*, Patterson 1975: fig. 112; *Lepidotes*, Patterson 1975: fig. 108), pachycormids (*Pachycormus*, Patterson 1975: fig. 106), pholidophorids and Lower Jurassic leptolepids, but it is obliterated in later leptolepids and living teleosts (Gardiner 1973: 111; Patterson 1975: 398).

Living chondrosteans and holosteans have a neuromast organ lodged near the top of the spiracular canal, supplied by the otic branch of the facial nerve. A similar neuromast sense organ occurs in selachians (Wright 1885), but here it is lodged in a closed vesicle which has become pinched off from the base of the spiracular cleft.

In *Latimeria* the spiracle lies free alongside the intracranial joint. It is closed dorsally and terminates just beneath the dermal roof. As in *Polypterus* (and holocephalans) there is no spiracular sense organ, but the overlying neuromast of the temporal canal is greatly enlarged (Forey, personal communication).

Eusthenopteron is the only rhipidistian in which there is clear evidence of a spiracular groove (Jarvik 1954: fig. 22, gr. psp.). The spiracle in lungfishes is rudimentary and no trace of it has been described in fossil dipnoans (Gardiner 1973: 113; Miles 1977). A spiracular sense organ (Pinkus' organ), however, is found in Recent dipnoans where it is lodged in the otic process of the palatoquadrate, and a deep fissure in front of the hyomandibular facet in Devonian dipnoans (Miles 1977: 79) may have housed a similar sense organ.

It is thus apparent that a bone-enclosed spiracular canal and sense organ is a synapomorphy of advanced actinopterygians, whereas the presence of the sense organ may be more general (selachians, later actinopterygians and dipnoans).

9. *Origin of dorsal hyoid constrictor muscle.* In living chondrosteans there is an undifferentiated dorsal hyoid constrictor which forms a continuous sheet of muscle and originates along the dorsolateral margin of the braincase from hyomandibular facet to auditory capsule. It inserts ventrally on the hyomandibula and opercular.

A similar constrictor hyoideus dorsalis is found in selachians and its dorsal portion inserts on the hyomandibula (Edgeworth 1935: 98). From this evidence we can assume that primitively in gnathostomes the hyomandibula was levated from above by the anterodorsal portion of the hyoid constrictor.

In the development of *Polypterus, Amia* and *Lepisosteus* the anterior edge of the hyoid constrictor spreads forwards internal to the hyomandibula to form the adductor hyomandibulae, and the posterior portion of the constrictor differentiates into the adductor operculi. In *Amia* and teleosts the constrictor hyoideus is still more elaborately differentiated. If *Polypterus* is the sister-group of the chondrosteans plus neopterygians then the adductor hyomandibulae must have evolved separately in at least two lines of Recent fishes. *Latimeria* (Millot & Anthony

1965), in which the adductor operculi lies dorsal to the adductor hyomandibulae, suggests yet another separate origin.

In the Gogo palaeoniscids there is a continuous dorsal muscle scar stretching from just behind the point of articulation of the hyomandibula to the occipital fissure, only interrupted by a groove for branches of the glossopharyngeal and vagus nerves. It is presumed that this elongate area gave rise to an undifferentiated dorsal hyoid constrictor muscle as in living chondrosteans. It is unlikely that any part of the dorsal hyoid constrictor had its origin in the conspicuous 'subtemporal fossa' (Gardiner 1973: fig. 3) as suggested by Patterson (1975: 395), since the whole of this fossa consists of fenestrated bone, totally unsuitable for muscle origin. This so-called 'subtemporal fossa' in the Gogo palaeoniscid results from the lack of ossification of the side wall of the braincase in the neighbourhood of the jugular vein and is not such a distinct feature as in pholidophorids and other teleosts. There is no obvious subtemporal fossa in any other palaeoniscid, living chondrostean or *Polypterus*, and in the latter fish the adductores hyomandibulae and operculi form a continuous muscle (Lauder 1980) which originates on the dorsolateral surface of the opisthotic.

In pholidophorids, leptolepids and other primitive teleosts the subtemporal fossa presumably served principally for the origin of the adductor operculi and there is usually an anterior, less well-marked depression for the origin of the adductor hyomandibulae. The first recognizable depression which may be considered to be the homologue of the subtemporal fossa of pholidophorids and teleosts is found in fossil neopterygians (parasemionotids, *Heterolepidotes, 'Aspidorhynchus', Dapedium, Lepidotes* and *Pachycormus*; Patterson 1975: figs 97–9, 102, 106, 108, 112) although in *Amia* and *Lepisosteus* there is no obvious subtemporal fossa.

In *Perleidus* (Patterson 1975: fig. 115) and *Australosomus* (Nielsen 1949: figs 2, 29) there is a large subtemporal fossa, but this is presumed to be the homologue of both the anterior depression and subtemporal fossa of fossil halecomorphs, pholidophorids and teleosts.

In summary, the subtemporal fossa appears to be a specialization of later actinopterygians which in halecomorphs and teleosts serves for the origin of the adductor operculi.

In *Latimeria* (Millot & Anthony 1965: fig. 31) the dorsal hyoid constrictor has differentiated into an adductor hyomandibulae and an adductor operculi. The origin of the adductor hyomandibulae is remote from the adductor operculi and below the jugular canal; by comparison with selachians and chondrosteans this condition is presumed to be derived, as is the double articulation of the head of the hyomandibula. In the Devonian *Nesides* a distinct fossa (Bjerring 1977: fig. 22, ar.m.ad.hy) below the jugular canal must have served for the origin of the adductor hyomandibulae and a more dorsal fossa behind the dorsal hyomandibular articulation contained the adductor operculi. Identical fossae are recognizable in the rhipidistians *Ectosteorhachis* (Romer 1937: fig. 2) and *Rhizodopsis*. In *Eusthenopteron* (Jarvik 1954: fig. 21A, B; 1975: fig. 13A, B) the so-called 'process for the attachment of adductor muscles of hyomandibula' (Bjerring 1971: fig. 8) forms the posterior boundary of a depression which, by analogy with *Nesides* and *Latimeria*, also served for the origin of the adductor hyomandibulae.

There is no adductor hyomandibulae in Recent dipnoans and it is likely that the loss of this muscle is correlated with the reduction of the functional importance of the hyomandibula following fusion of the palate with the braincase.

10. *Origin of dorsal mandibular constrictor muscle*. The constrictor dorsalis is undifferentiated in living chondrosteans (Edgeworth 1935: 48), where it forms a large and powerful protractor hyomandibularis which originates dorsally on the postorbital process. A similar constrictor dorsalis is also characteristic of selachians where it has its origin on the postorbital process and extends downwards to insert on the inner (medial) surface of the palatoquadrate. In selachians it is called the levator maxillae.

In *Polypterus* the constrictor dorsalis has differentiated into four distinct muscles, the levator arcus palatini, protractor hyomandibularis, dilatator operculi and musculus spiracularis (Allis 1922: 254), but in all living neopterygians it differentiates into only two muscles (Lauder 1980), the levator arcus palatini and the dilatator operculi, with the posterior portion of the levator arcus palatini inserting on the hyomandibula (= protractor hyomandibularis).

From this evidence it is clear that primitively in actinopterygians the posterior portion of the constrictor dorsalis (levator arcus palatini) was attached to the hyomandibula. The condition in living chondrosteans, where the anterior portion of the levator arcus palatini is missing, must be considered derived and related to the reduction of the palatoquadrate and its loss of contact with the braincase. In *Polypterus* the levator arcus palatini and protractor hyomandibularis originate together, the levator arcus palatini inserting on both the dorsal edge of the entopterygoid and the hyomandibula while the protractor hyomandibularis also inserts (via a membrane) on the dorsal edge of the palatoquadrate and the anterior edge of the hyomandibula. Both of these muscles, in being inserted to the suspensorium, may be equated with the single levator arcus palatini of neopterygians. The presence of separate levator arcus palatini and protractor hyomandibularis muscles in *Polypterus* is considered derived and related to the reduction of the posterodorsal corner of the palatoquadrate (otic process), which has allowed part of the levator arcus palatini to insert on the hyomandibula and then eventually to separate off as a distinct muscle. A separate protractor hyomandibularis is not seen in any other living fish (other than chondrosteans: see above) and it is doubtful that one existed in rhipidistians as postulated by Jarvik (1954: fig. 26).

There is no evidence of separate areas for the origins of dilatator operculi and levator arcus palatini muscles in any palaeoniscid and it is unlikely that these muscles differentiated. The constrictor dorsalis is postulated to have originated on the postorbital process, much as in *Polypterus* and selachians. With the elongation of the spiracular canal in more advanced actinopterygians a new area was made available for the hyoid constrictor, anterior to and above the hyomandibular facet. This area, first recognizable in *Perleidus* and parasemionotids, is termed the dilatator fossa. In lepisosteids, halecomorphs and pholidophorids the anterior area of the dilatator fossa housed the levator arcus palatini and the posterior area the dilatator operculi. In leptolepids (Patterson 1975: 387) the dilatator fossa only housed the dilatator operculi as in Recent teleosts, and is separated by a crest of bone from the area of origin of the levator arcus palatini.

In *Latimeria* (Millot & Anthony 1958) the dorsal constrictor has apparently differentiated into two muscles much as in neopterygians. The so-called 'levator arcus palatini' runs from in front of the dorsal hyomandibular facet to insert on the hind edge and inner (medial) surface of the palatoquadrate. The partial insertion of this muscle on the inner palatoquadrate surface is considered primitive for osteichthyans and gnathostomes, while the condition in actinopterygians, where the levator arcus palatini inserts on the outer surface of the palate, is derived. The effect this different origin has on elevation of the palate has been commented on elsewhere (Gardiner 1973: 121). It suffices to add that the action of the 'levator arcus palatini' in *Latimeria* merely pulls the palatoquadrate inwards and backwards. Anteriorly the 'levator arcus palatini' originates on the prootic behind the spiracle, not on the postorbital process as in selachians and actinopterygians. The dilatator (elevator) operculi in *Latimeria* is a small muscle lying just behind the 'levator arcus palatini' and which has presumably evolved in parallel with that in actinopterygians. It is difficult to see where the dorsal constrictor would have inserted in rhipidistians, but by comprison with actinistians, it must have originated behind the spiracular groove on the anterodorsal face of the lateral commissure. In *Eusthenopteron* (Jarvik 1954: fig. 23) the constrictor dorsalis could only have originated on the lateral commissure just anterior to the post-temporal fossa; in *Ectosteorhachis* (Romer 1937: figs 2, 6) and *Rhizodopsis* there is a well-marked depression in this area.

In dipnoans the constrictor dorsalis has not separated from the adductor mandibulae (cf. holocephalans) and this is considered a specialization related to autostyly (Miles 1977: 121).

11. *Endolymphatic duct.* In *Acipenser* the endolymphatic organ is club-shaped and extends into the cranial cavity, but in *Polypterus, Lepisosteus, Amia* and most teleosts it is shorter and confined to the otic capsule. In *Mimia* there is a gutter running from near the junction of the posterior semicircular canal with the sinus superior to the dorsal surface of the cranial cavity in

front of the dorsal fontanelle. This must have housed the blind-ending endolymphatic organ. In *Moythomasia*, on the other hand, the gutter for the endolymphatic duct opens into the posterior dorsal fontanelle and the duct was probably still open, as in chondrichthyans, placoderms and Devonian dipnoans. Unfortunately in one specimen of *Mimia* figured by Gardiner (1973: fig. 4, mcc) the area of the braincase around the end of the endolymphatic ducts had not completely ossified and this, together with the report of a median intramural chamber in *Dapedium* (Patterson 1975: 413), led Miles (1977: 102) to postulate the presence of a median supraotic cavity in actinopterygians. However, there is no such cavity in any living chondrichthyan, actinopterygian or *Latimeria* and it is better regarded as a specialization confined to some dipnoans, rhipidistians and tetrapods.

The endolymphatic duct is primitively open in gnathostomes and its closure in actinopterygians is considered a specialization. There is no evidence of a hypertrophied endolymphatic sac in actinopterygians.

Miles (1977: 103) has argued that the anterior division of the so-called supraortic cavity of primitive dipnoans is a synapomorphy shared with choanates. However, Young (1980: fig. 10) has described what he considers to be a posterior 'endolymphatic diverticulum' in the placoderm *Brindabellaspis* and states that this shows some resemblance to the supraortic cavity of Devonian dipnoans. But the supraortic cavity of rhipidistians and choanates is related to the endolymphatic duct which passes through it onto the roof of the neurocranium, and is primitively divided into a posterior median division and an anterior paired division. The 'endolymphatic diverticulum' of *Brindabellaspis* has none of these features and can in no way be homologized with the supraortic cavity.

12. *Pterosphenoid pedicel.* Patterson (1975: 409) proposed that this was a primitive actinopterygian feature, mainly because he recognized the relationship of this structure to the intramural chamber for the superficial ophthalmic nerves in *Kentuckia, Kansasiella* and caturids. From the condition in *Moythomasia* (see p. 230) it is now more certain that he was correct in homologizing the upper part of the pterosphenoid pedicel with that intramural chamber.

In *Moythomasia* (Fig. 29) the pedicel is often only partially developed, much as in *Pteronisculus magnus* (Nielsen 1942: 90) and Kansas palaeoniscid B (Watson 1925: 843), but in some specimens of *Moythomasia* (Fig. 30) it is complete and the lower portion is believed to have been formed by the prootic, as in *Macrepistius* (Schaeffer 1971: fig. 4). A similar pedicel is seen in *Amia* and its fossil relatives but here it is formed entirely by the pterosphenoid and meets the ascending process of the parasphenoid ventrally. In other caturids only the dorsal portion of the pedicel is present (*'Aspidorhynchus'*, Patterson 1975: fig. 101) or sometimes only that part which envelops the superficial ophthalmic nerves (*Caturus, Heterolepidotus, Osteorachis*). In the larger pholidophorids (Patterson 1975: 409) the upper pterosphenoid portion is often present while in the Sinemurian *Leptolepis* only the lower prootic portion is developed. As in Recent teleosts, however, where the pedicel is frequently well developed, it consists mainly if not entirely of membrane bone.

From this we may conclude that the presence of a pterosphenoid pedicel is primitive, at least for actinopterygians, whereas enclosure of the superficial ophthalmic nerves in a separate bony canal is possibly a primitive osteichthyan feature (cf. *Youngolepis*).

13. *Prootic bridge and posterior myodome.* In vertebrate embryos the relationships of the orbital cartilage are surprisingly constant. Posteriorly it is invariably attached to the polar cartilage (or trabecula) by a pila antotica. The bases of the pilae antoticae are joined by a transverse connective cartilage, the acrochordal, which eventually forms the crista sellaris, dorsum sellae or prootic bridge.

In selachians (*Pristiurus*, Matveiev 1925: fig. 2; *Scyllium*, de Beer 1937: 69; *Squalus*, Holmgren 1940: 94; *Torpedo*, de Beer 1937: 69), dipnoans (*Neoceratodus*, Sewertzoff 1902: fig. 1) and amphibians (*Ambystoma*, Stöhr 1879) the orbital cartilage and pila antotica develop early, whereas in actinopterygians (*Polypterus*, Moy-Thomas 1934; *Acipenser*, Sewertzoff 1928;

Lepisosteus, Hammarberg 1937; *Amia*, Pehrson 1922; *Salmo*, de Beer 1927) these structures develop later and lag behind the auditory capsule, polar cartilage and trabecula. In selachians the dorsum sellae appears early, but in actinopterygians its development is considerably delayed, often until after the lateral walls of the braincase are completed. This delay in actinopterygians is often attributed to the development of the myodome, but the dorsum sellae is equally delayed in *Polypterus* and *Acipenser*, fishes without a myodome.

We now know that there are palaeoniscids without a posterior myodome (*Mimia, Moythomasia*) and that this was probably the primitive condition for actinopterygians (Gardiner 1973; Gardiner & Bartram 1977). We also know that the relationships of the profundus are quite varied (see above), but that bone in the position of the pila antotica always separates the trochlear, optic and oculomotor nerves from the trigeminal foramen. It is difficult then to concede that, because of the varying relationships of the profundus, the pila antotica is a secondary structure in *Polypterus, Acipenser*, and *Salmo* as de Beer (1937) and Schaeffer (1971: 6) assumed. It is even more difficult to accept its absence in *Lepisosteus* (de Beer 1937), where the difference is that the pila antotica lies somewhat more anteriorly than in other forms.

The dorsum sellae is assumed to have been ossified by the basisphenoid in *Mimia* (Gardiner & Bartram 1977: 230) and *Moythomasia*, as in *Polypterus*, but in all other actinopterygians it is formed by the prootics. The abducens nerve passes out below the dorsum sellae in *Mimia, Moythomasia* and *Polypterus*, behind it in *Acipenser*, in front and above in *Lepisosteus* (where the myodome is assumed to have been secondarily lost – see below), whereas in all other actinopterygians where a myodome is present the abducens pierces the prootic bridge.

An ossified prootic bridge (dorsum sellae) is also present in the anterior moiety of the braincase of actinistians and rhipidistians (Romer 1937, Thomson 1967, Schaeffer 1968) and is not missing as erroneously suggested by Gardiner (1973: 108). The lateral wall of the neurocranium of *Latimeria* is presumed to exhibit the primitive gnathostome condition, with the profundus, trochlear, optic and oculomotor nerves all passing through separate canals. The dorsum sellae is ossified by the basisphenoid and this bone also contains the foramina of the oculomotor and profundus nerves, as in *Polypterus*, whereas the abducens nerve leaves the braincase behind the dorsum sellae as in *Acipenser*.

In the rhipidistians *Ectosteorhachis* (Romer 1937: fig. 2) and *Eusthernopteron* (Jarvik 1954: fig. 1c) it may be inferred that the dorsum sellae, as in *Latimeria* and *Nesides*, is ossified by the basisphenoid and that the abducens nerve did not pass through it.

The dorsum sellae is cartilaginous in Recent dipnoans but ossified in the Devonian forms. In *Griphognathus* the profundus is supposed to pass out below and behind the dorsum sellae (Miles 1977: fig. 10), but this canal (V_1) could be more convincingly interpreted as transmitting the abducens nerve. In *Chirodipterus* the dorsum sellae lies further posteriorly than in *Griphognathus*, the profundus passed out above it, and the canal for the abducens (Miles 1977: figs 17, 35) is said possibly to originate between the facial and trigeminal canals, above the dorsum sellae.

In chondrichthyans such as *Heterodontus, Torpedo* and *Hydrolagus* the dorsum sellae is a stout bar of cartilage and the abducens nerve exits with the trigeminal above and slightly behind it. In *Squalus*, however, the abducens leaves through a separate canal below and posterior to the dorsum sellae (Jollie 1962: fig. 5.10).

In the placoderms *Buchanosteus* (Young 1979: figs 5, 6) and *Kujdanowiaspis* (Stensiö 1963*b*: fig. 26) the abducens has a separate canal which leaves the brain behind the root of the trigeminal, much as in *Squalus*.

I conclude that primitively in osteichthyans the dorsum sellae was ossified by the basisphenoid bone and in the primitive gnathostome the abducens nerve passed out below and behind it.

Posterior myodomes are not present in the primitive actinopterygian braincase (*Polypterus*, living chondrosteans) and are also absent in the Gogo palaeoniscids. There is little doubt that at least three of the rectus muscles originated on the basisphenoid pillar in *Mimia* and *Moythomasia* (Gardiner & Bartram 1977: 237), but whether or not the external rectus muscle originated here or in the back of the orbit ventrolateral to the abducens canal could not be determined, though it seems unlikely that it originated posteriorly. In *Polypterus* three of the muscles (superior, inferior and external recti) arise from a short tendinous stalk with its origin on the basisphenoid immediately posterior to the optic foramen in a homologous position to those in selachians, while the fourth (internal rectus) takes origin anterior to the optic foramen. Similarly in *Acipenser* the four recti muscles attach to the cartilaginous interorbital region. The rectus muscles also originate on the basisphenoid in *Latimeria*, and a distinct pit in front of the basipterygoid process in *Holoptychius* (Jarvik 1972: fig. 20B) and *Youngolepis* (Chang 1982: fig. 15B) must also have served for the origin of all four muscles. In *Acanthodes* (Miles 1973*a*: fig. 9; Jarvik 1977: fig. 3A) the perichondrally ossified basisphenoid pillar may have been related to these muscles. Primitively in gnathostomes the rectus muscles originated on the interorbital septum posterior to the optic nerve. In *Lepisosteus* the origins of all four rectus muscles have moved onto the basipterygoid process (which is made up of the prootic; the basisphenoid is absent) and this is considered to be a specialization, as are the path of the abducens nerve and the loss of the myodome. In *Amia*, on the other hand, the superior, internal and inferior recti muscles originate on the transverse bolster of the basisphenoid and the external rectus enters the myodome. Myodomes only occur in more advanced actinopterygians (*Amia* and teleosts among living fishes), presumably as a result of the backward growth of the external rectus muscles onto that area of the basisphenoid immediately below and lateral to the pituitary.

In *Kentuckia* the myodome is represented by small paired depressions lateral to the pituitary vein foramen and ventral to the abducens canal. The ventral otic fissure lies more posteriorly than in *Mimia* or *Moythomasia* and I have argued elsewhere (Gardiner 1973: 106; Gardiner & Bartram 1977: fig. 8) that this is a consequence of the enlargement of the myodome (but see Schaeffer & Dalquest 1978); the larger the muscle canal is, the further back lies the fissure (see also Patterson 1975: 543). With this increase in size of the myodome the ventral otic fissure migrated further posteriorly until it became confluent with the vestibular fontanelles, and the enlarged dorsum sellae, which in *Mimia* and *Moythomasia* is ossified by the basisphenoid, is now ossified by the prootic. Consequently the ventral otic fissure is represented by the prootic/basioccipital suture, not the basisphenoid/basioccipital suture as in the Gogo palaeoniscids and *Polypterus*. Alternative explanations are provided by Schaeffer & Dalquest (1978) and Bjerring (1978).

14. *Anterior and middle cerebral veins.* Primitively, both these veins were well developed in actinopterygians, the anterior cerebral vein leaving the telencephalon recess high up through a transversely-directed canal in front of the epiphysial crest and trochlear nerve, whereas the middle cerebral vein left the cranial cavity through the metencephalic recess (*Mimia, Polypterus*) or the recess for the optic lobe (*Pteronisculus, Moythomasia*) but always behind the trochlear foramen.

Canals for the anterior and middle cerebral veins are present in *Mimia, Moythomasia, Kansasiella* (Poplin 1974: fig. 20, v, v.cer.ant), *Pteronisculus* (Nielsen 1942: fig. 6, v, v.cer.ant) and *Polypterus* (Allis 1922: 228), and in *Polypterus* both veins run into the supraorbital vein as in larval *Lepisosteus* (Hammarberg 1937: figs 25–27).

Despite the fact that the middle cerebral vein fails to develop in *Amia* (Bertmar 1965) and the anterior cerebral vein is absent in adult *Lepisosteus*, both veins were present in parasemionotids, *Caturus, Heterolepidotus, 'Aspidorhynchus', Macrepistius, Dapedium, Lepidotes, Pachycormus*, pholidophorids and leptolepids (Patterson 1975: 412). Both veins occur in most living teleosts but according to Bertmar (1965: 122) and Patterson (1975: 411) have migrated to a more posterior position during the ontogeny and phylogeny of the group; the middle cerebral vein now falls into the jugular vein.

The position of the anterior cerebral vein in non-teleostean actinopterygians is remarkably constant but the same cannot be said for the middle cerebral vein. Primitively the canal for the middle cerebral vein originated in the optic recess above the trigeminal canal and behind the trochlear foramen. It passed down through the pterosphenoid to emerge in the orbit below and behind the pterosphenoid pedicel in the roof of the ganglion recess (for the gasserian and lateralis ganglia), close to the opening of the superficial ophthalmic canal. This is the condition seen in *Moythomasia* and most caturids; also in pholidophorids and leptolepids except that in

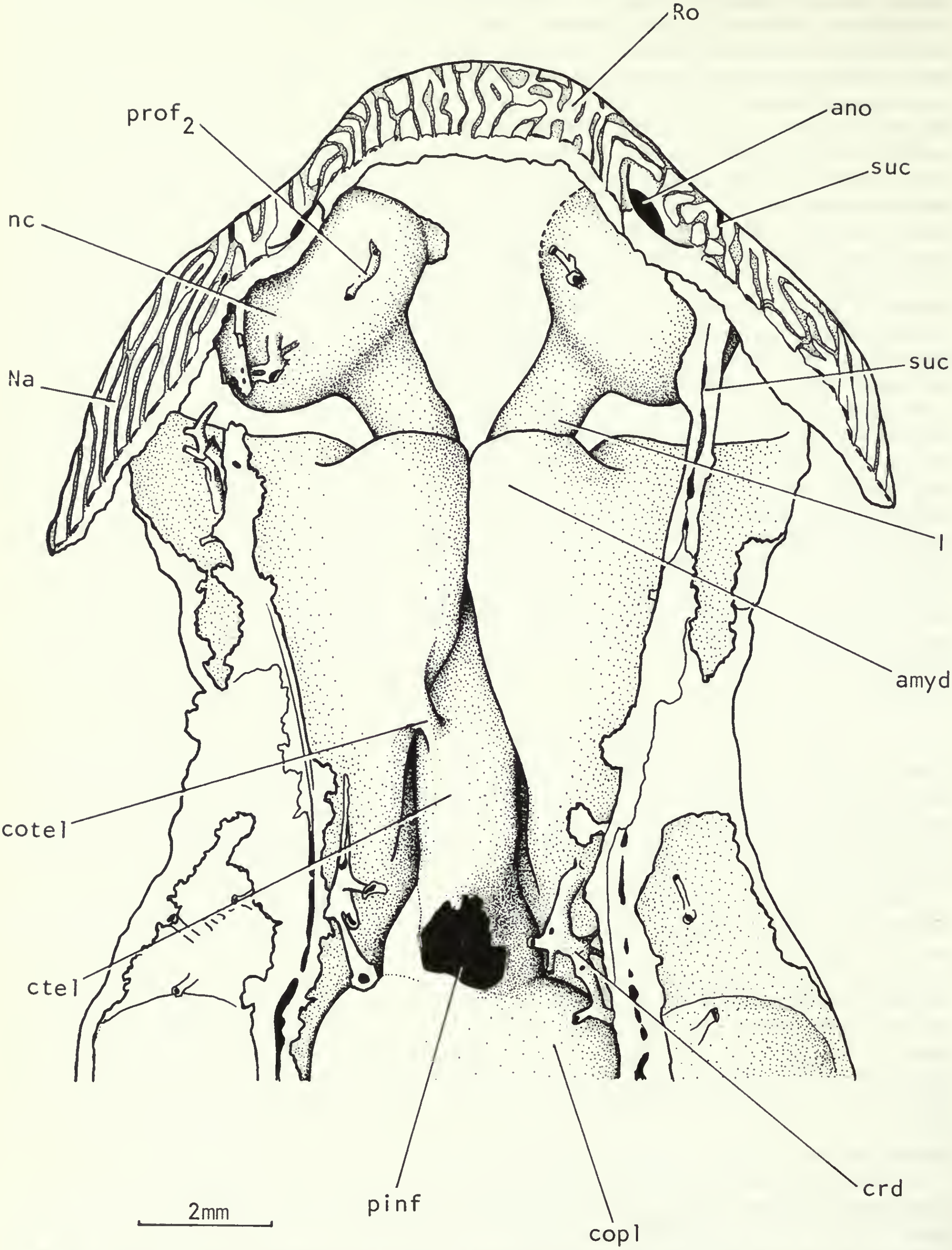
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Fig. 33 *Mimia toombsi* Gardiner & Bartram. Preserved orbitotemporal and ethmoid parts of the neurocranium and attached dermal bones, in dorsal view, from BMNH P.56476.

the latter two groups the ophthalmic canal is missing and the foramen for the middle cerebral vein opens in line with the groove for the superficial ophthalmic nerves.

Thus primitively the trigeminal and middle cerebral vein canals lay close together (see particularly *Mimia*) and consequently it is not surprising to find the former capturing the latter in many teleosts.

In *Latimeria* the anterior cerebral vein leaves the cranial cavity through a separate foramen in the anterior wall of the orbit and falls into the supraorbital vein (Millot & Anthony 1958; Robineau 1975: 46) much as in *Polypterus*. There is, however, doubt as to whether or not a true middle cerebral vein occurs. Millot & Anthony (1958: fig. 5) indicated a middle cerebral vein passing behind the dorsal prefacial process of the prootic and running into the jugular vein immediately in front of the jugular canal, whereas Robineau (1975) said it was absent, adding that the ventrolateral sinus which lies in the posterior cranial cavity between the dura mater and cranial wall is its likely homologue. If a true middle cerebral vein is present in *Latimeria* then by comparison with actinopterygians it would pass out between the two parts of the cranium with the trigeminal nerve, as reported by Millot & Anthony (1958).

In *Neoceratodus* the anterior cerebral vein is much as in *Latimeria* and actinopterygians, passing through a separate foramen in the orbital wall and falling into the supraorbital vein (Spencer 1893: fig. 15). In the Devonian dipnoan *Griphognathus* Miles (1977: fig. 61) has demonstrated an extensive epiphysial plexus similar to that reported in *Latimeria* (Robineau 1975: 46) and in one specimen found a pair of foramina in the orbitotemporal for the exit of two branches of the anterior cerebral vein (cf. *Torpedo*, Holmgren 1940: fig. 154). In *Chirodipterus*, however, Miles (1977: figs 17, 47; see also Stensiö 1963*b*: fig. 43c) has also demonstrated the presence of a perichondrally-lined canal passing posterolaterally under the utricular recess and opening into the jugular canal, which undoubtedly housed the middle cerebral vein in life. Although other workers (*Chirodipterus*, Säve-Söderbergh 1952: fig. 6; *Dipnorhynchus*, Thomson & Campbell 1971: fig. 32) have restored the canal for the middle cerebral vein to a more dorsal position, all agree that it lies behind the facial and trigeminal canals. This must be a dipnoan specialization since primitively in osteichthyans the middle cerebral vein leaves the cranium in front of the trigeminal nerve or between the trigeminal and facial nerves (*Mimia, Ectosteorhachis*).

In rhipidistians a canal for the anterior cerebral vein has been described in *Rhizodopsis* (Säve-Söderbergh 1936), *Ectosteorhachis* (Romer 1937: fig. 8, unlabelled) and *Eusthenopteron* (Stensiö 1963*b*: fig. 50A). In *Ectosteorhachis* (Romer 1937: fig. 8) there was also an anastomosis between the anterior cerebral veins reminiscent of the epiphysial blood plexus of *Latimeria, Griphognathus* and the embryonic stages of actinopterygians and selachians. The path of the middle cerebral vein in *Ectosteorhachis* is represented by a large canal which lies below and between the trigeminal and facial canals and opens into the jugular trough. A narrower canal in a similar position has also been dscribed in *Glyptolepis* (Jarvik 1972: fig. 21B). On the other hand in *Eusthenopteron* Bjerring (1971: fig. 17) has suggested that the middle cerebral vein passed dorsal to the trigeminal canal as in actinopterygians (see also Jarvik 1980: 186).

In selachians the anterior cerebral vein is as in osteichthyans whereas the middle cerebral vein, which in development passes in front of the root of the trigeminal nerve (Holmgren 1943: fig. 57, v.c.int; Bertmar 1965: fig. 9), passes through the trigeminal foramen with the trigeminal nerve in the adult and falls into the jugular vein (cf. teleosts).

15. *Sclerotic bones*. In *Mimia* the sclerotic ring may be comprised of two, three or four segments, or may be a complete ring. The only possible explanation for these varying conditions is to assume that there were always four ossification centres and that ontogenetic fusion occurred. Similarly in *Pteronisculus*, where there are normally four segments, three have been recorded in some instances (Nielsen 1942), and in *Moythomasia* there may be two segments (*M. durgaringa*) or four (*M. nitida*, Jessen 1968). The majority of palaeoniscids also have four segments (*Cheirolepis, Watsonichthys, Mesonichthys, Nematopychius, Amblypterus, Gonatodus, Cornuboniscus, Paramblypterus, Commentrya, Birgeria*). There are also four sclerotics in *Australosomus, Lawnia, Chondrosteus, Acipenser, Dorypterus, Bobasatrania* and some

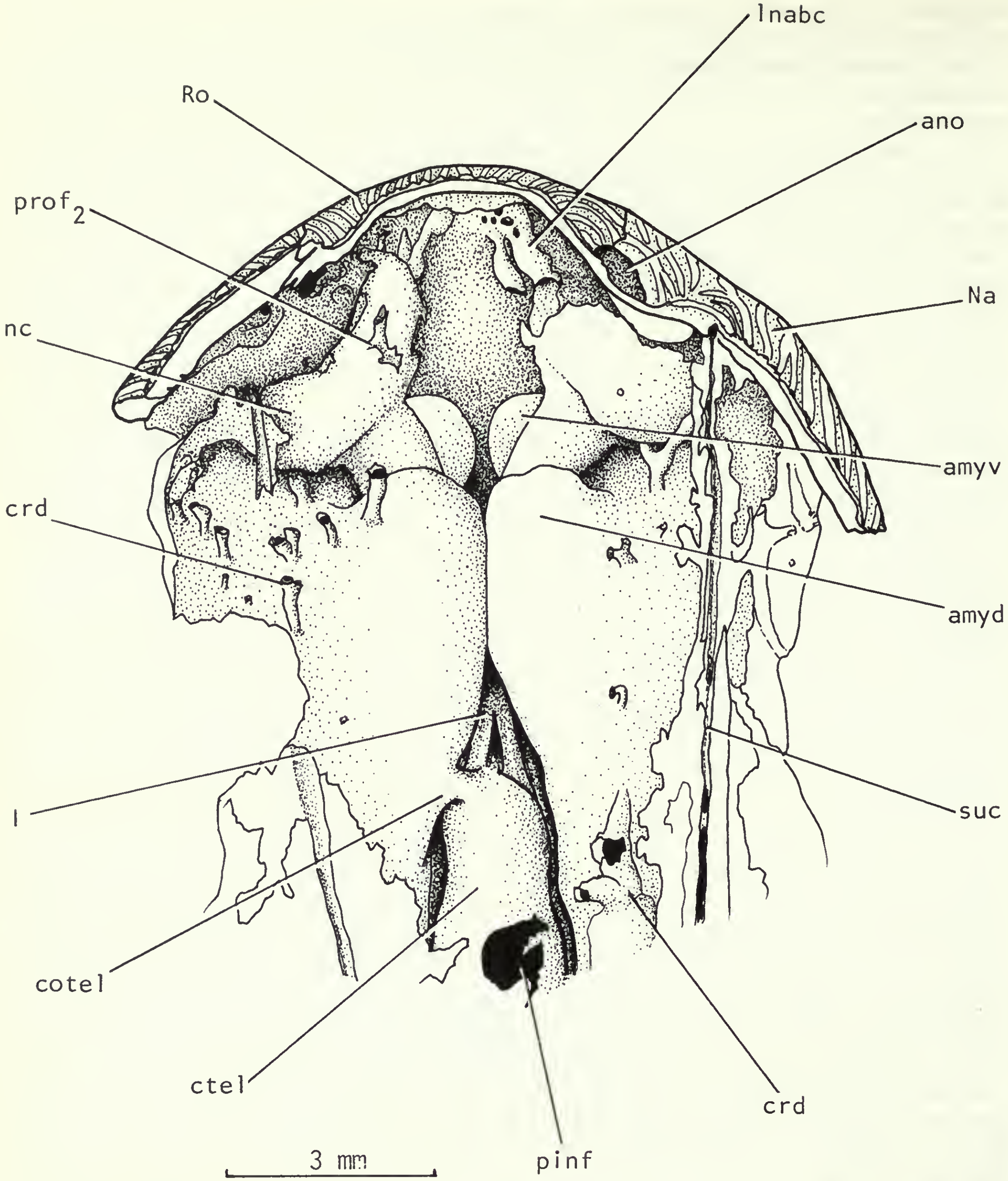

Fig. 34 *Mimia toombsi* Gardiner & Bartram. Preserved ethmoid region of the neurocranium and attached dermal bones, in dorsal view, from BMNH P.56505.

pholidophorids, but in *Pholidophorus macrocephalus*, leptolepids and other teleosts there are only two (Patterson 1975: 414). There are similarly two segments in fossil actinopterans such as *Lepidotes* and *Dapedium* (Edinger 1929) and in *Aspidorhynchus, Pachycormus, Mesturus* and *Macromesodon*. From this evidence we may conclude that a sclerotic ring composed of four segments is primitive for actinopterygians.

Elsewhere within the osteichthyans the number of segments is much greater. Thus in

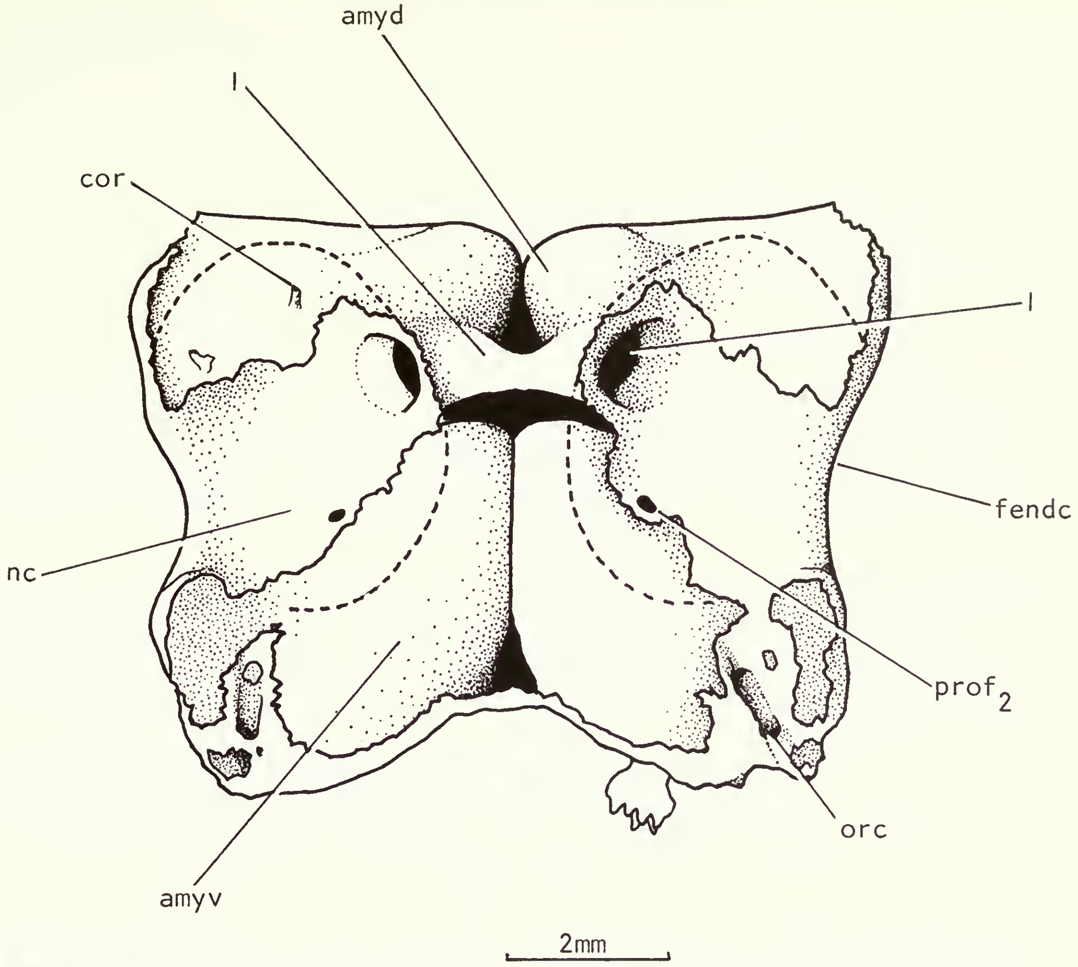

Fig. 35 *Mimia toombsi* Gardiner & Bartram. Ethmoid region in anterior view, from BMNH P.53240. Broken lines denote limits of nasal capsules.

actinistians there are 18 to 20 in *Latimeria* (Millot & Anthony 1965). There are approximately 18 in the onychodont *Strunius* (Jessen 1966), 17 in the rhipidistian *Osteolepis*, and in *Eusthenopteron* as many as 35 segments (Jarvik 1944*a*). Within the dipnoans similar large numbers have been recorded in *Rhinodipterus* and *Dipterus* (more than 20 in each; Schultze 1970), but in the Devonian *Griphognathus* Miles (1977: 249) has described a single undivided ring. Miles decided this was 'a specialized feature brought about by the late ontogenetic fusion of numerous segments'.

Elsewhere in gnathostomes a sclerotic ring occurs in placoderms and acanthodians. In the latter group it always appears to comprise five segments (*Acanthodes, Protogonacanthus, Homalacanthus, Triazeugacanthus*, Miles 1965, 1966; *Cheiracanthus, Mesacanthus*, Watson 1937) but in placoderms the number is usually four (*Phlyctaenaspis, Arctolepis* Heintz 1962: 36; *Coccosteus, Holonema* Miles 1971*b*: 141). Only three have been recorded in *Bothriolepis* (Stensiö 1948) but in the rhenanids *Gemuendina* and *Jagorina* there are as many as 10 and 12 segments respectively (Stensiö 1950). In *Goodradigbeeon* (White 1978: 196) there is a circlet of four dermal plates but a further dermal plate articulates with part of the inner margin of this ring and an almost complete layer of perichondral bone covered both surfaces of the calcified sclerotic cartilage (see BMNH P.33734, P.50455). Although the so-called sclerotic ossifications recorded in the agnathans *Jamoytius* and *Lasanius* (Ritchie 1968: 21) appear to be no more than the remains of the pigmented retina, and in other anaspids are probably circumorbital scutes (Janvier 1981: 137), distinct sclerotic bones occur in a number of celphalaspids (Janvier 1981) and both dermal and perichondral elements can be recognized in specimens of *Atelaspis* (*Aceraspis*) *robusta* (BMNH P.2138) and *Hemicyclaspis* (BMNH P.8809, P.8801). These apparently number four segments.

A sclerotic ring is thus a synapomorphy of advanced 'agnathans' and gnathostomes and which in gnathostomes and cephalaspids primitively consisted of four segments.

A sclerotic ring of more than 12 segments is a synapomorphy of osteolepids, actinistians, onychodonts, porolepids and choanates.

Ethmoid region and associated dermal bones

The ethmoid region is well preserved in *Mimia* and the cartilage was entirely enclosed in a thin layer of perichondral bone. Such a layer also lines the cavities of the nasal capsules and the many canals. There was no endochondral ossification in the ethmoid region. The perichondral bone is closely applied to the overlying dermal bones except in the region beneath the premaxillae and the anterior part of the rostral.

Mimia toombsi

The orbital face of the postnasal wall is shown in Fig. 36; it is divided sagittally by the very thin interorbital septum. This septum widens in the dorsal region where the paired, diverging perichondrally-lined canals of the olfactory nerves pass into the ethmoid region. There is an elongated dorsolateral gap in the ossification of this canal (gI, Figs 13, 36), as in *Boreosomus* (Nielsen 1942: fig. 62).

Above and below the olfactory nerves are pairs of depressions in the postnasal wall. The lower pair (amyv, Figs 13, 36, 40) have a greater rostral extent than the upper pair (amyd, Figs 13, 36, 40). A similar set of depressions is present in *Boreosomus* (Nielsen 1942: fig. 65) and *Pteronisculus* (Nielsen 1942: fig. 17). These depressions must be anterior myodomes as Nielsen suggested, the dorsal pair for the superior oblique muscles and the ventral pair for the inferior oblique muscles.

The wall separating the dorsal myodomes in *Mimia* is pierced by a few minute holes. Much larger apertures are found in a corresponding position in other primitive actinopterygians. Thus in *Boreosomus* (Nielsen 1942: fig. 62) there is a large fenestra connecting each pair of myodomes. In *Saurichthys* (Stensiö 1925: fig. 10B), where the anterior myodomes are very shallow, there are fenestrae in a similar position to those of *Boreosomus*, and the interorbital septum dividing the single anterior myodome of *Australosomus* (Nielsen 1949: fig. 2) is also pierced by a large fenestra.

Another conspicuous feature of the postnasal wall is a pair of marked lateral notches slightly below the level of the olfactory nerve canals. Such notches occur in *Pteronisculus* and *Kansasiella*, and mark the lateral limits of the fenestra endonarina communis, described below.

The paired articulation for the palatoquadrate cartilage faces posterolaterally at the junction of the postnasal wall and suborbital shelf.

The anterodorsal corner of the orbit and the postnasal wall are pierced by a large number of pores, many more than have been recorded in other primitive osteichthyans, and they form three groups. The first consists of canals leading from the anterodorsal corner of the orbit and dorsolateral parts of the dorsal anterior myodomes to the skull roof (nasals), the second of canals leading from the upper part of the postnasal wall to the cavity of the nasal capsule, and the third of canals leading from the lower part of the postnasal wall to the nasal cavity, to the premaxillae and rostral bones and to the nasobasal canals (see below).

The canals of the first group are of variable calibre and occur medial and lateral to the supraorbital sensory canal (crd, Figs 34, 36; cor, Figs 35, 36, 40). There are at least nine such canals on the left side and fewer on the right in BMNH P.56505, an acid-prepared specimen on which most of the following description is based. The most posterior of these canals leads to the

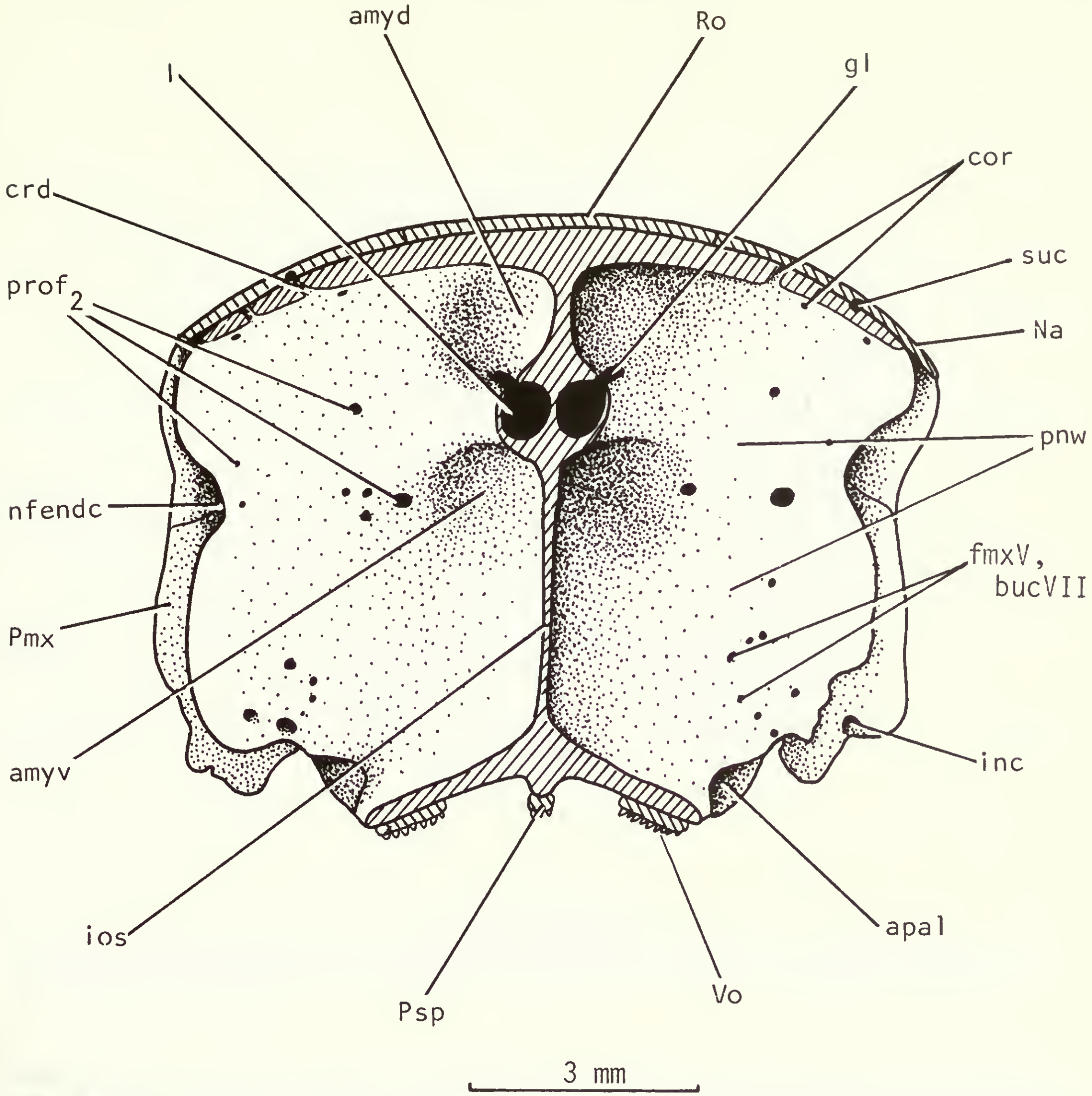

Fig. 36 *Mimia toombsi* Gardiner & Bartram. Braincase and associated dermal bones as if cut transversely through anterior region of orbit, to show the postnasal wall in posterior view; cut surfaces cross-hatched. From BMNH P.56505.

supraorbital sensory canal. This sensory canal lay in an open groove, bounded by raised walls, beneath the nasal bone. The raised walls fitted in turn into a groove, lined with perichondral bone, on the dorsal surface of the neurocranium. The canal connected with this groove and presumably conveyed branches of the superficial ophthalmic nerve. The remaining canals presumably carried other branches of the superficial ophthalmic nerves to the skull roof.

The canals of the second group are also asymmetrical in number in BMNH P.56505. On the left side one canal passes through into the posterior wall of the nasal capsule. Below this are four canals which pass slightly dorsally into the posteroventral corner of the cavity. Finally, two fine canals pass into the nasal capsule close to the lateral notch in the postnasal wall. On the right side the dorsal canal is symmetrical in position to that on the left side, but there is only one lateral canal and two ventral canals. Of the last two the lateral canal is the largest in the group. These orbitonasal canals are assumed to have carried branches of the profundus nerve.

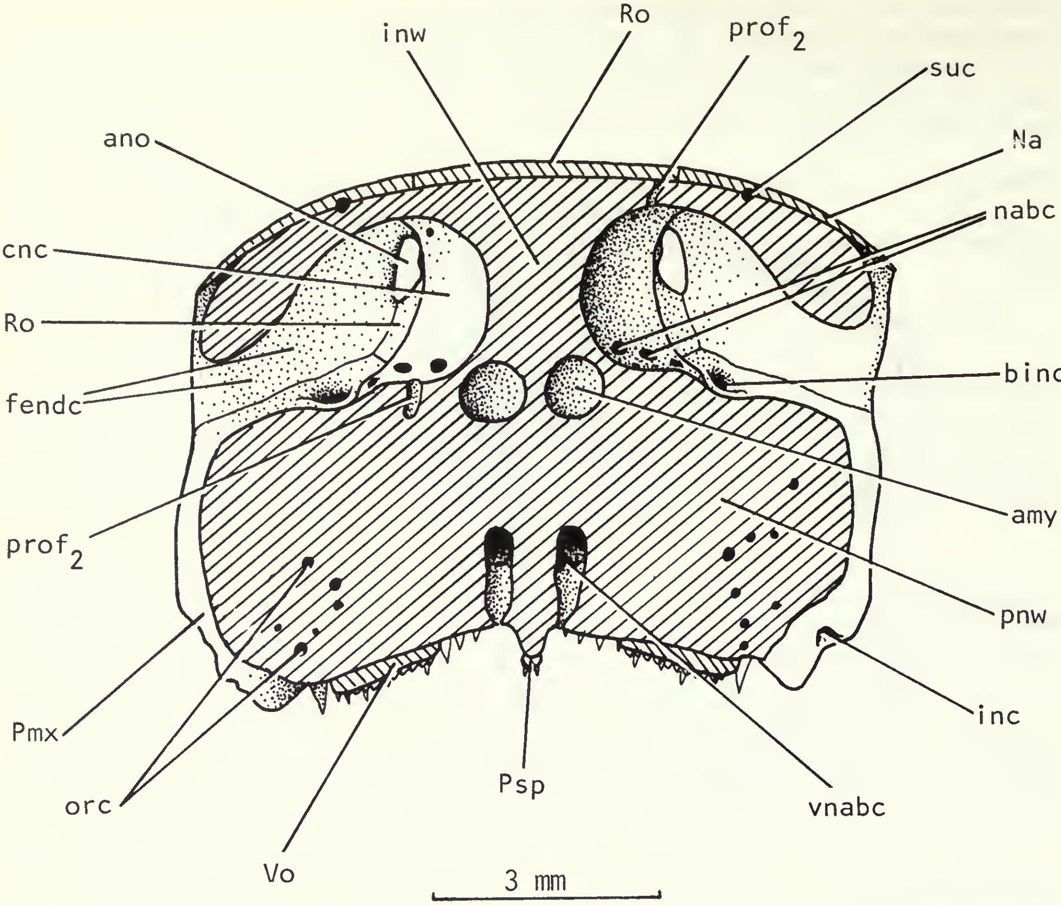

Fig. 37 *Mimia toombsi* Gardiner & Bartram. Braincase and associated dermal bones as if cut transversely through the nasal capsules, and viewed from the rear, from BMNH P.56505. Cut surfaces cross-hatched.

The pores of the ventral group are also asymmetrical in distribution, and in the directions which their corresponding canals take. Although these canals are visible for most of their length, their exact anterior limit and their minute terminal branches are not always clear. To investigate them more fully would involve further damage to the specimen: the specimen which was serially sectioned was deficient in this region. On the right side is an arc of six pores and two pores respectively dorsal and lateral to these. The lowermost pore of the arc passes anteromedially into a groove on the neurocranium running in the same direction, just above the tooth row of the premaxilla. Canals from the three following dorsal pores in the arc run into this groove, which appears to end near the tip of the rostral bone. The groove is remote from the more lateral infraorbital sensory canal in the premaxilla, but nerve endings could have crossed the gap between the neurocranium and the dermal bone. The next pore in the series leads to a dorsally-directed canal which connects with the central of the three anterior nasobasal canals described below. This canal sends fine branches to the infraorbital sensory canal. The canal associated with the most dorsal pore of the arc is short and leads into the same sensory canal. The pore dorsal to the group just described leads to a dorsally-directed canal which anastomoses with the lateral anterior nasobasal canal. Finally, the lateral pore forms a short canal leading to the infraorbital sensory canal.

On the left side is an arc of five pores and one lateral to these. The lowermost leads to a canal

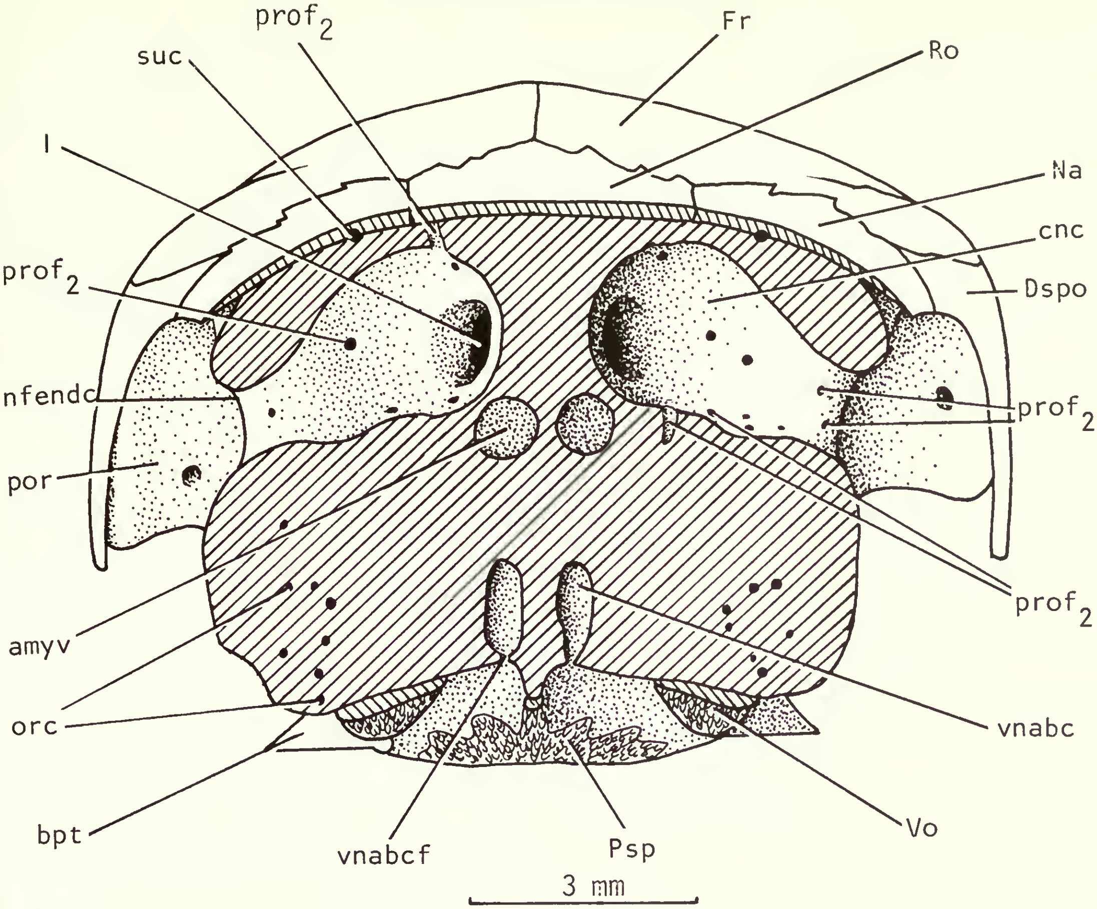

Fig. 38 *Mimia toombsi* Gardiner & Bartram. Braincase and associated dermal bones as if cut transversely through the nasal capsules, and viewed from the front, from BMNH P.56505. Cut surfaces cross-hatched.

and groove corresponding to that described on the right side. The next dorsal canal appears to turn into this groove while the third canal in the series runs parallel to the second and also joins the groove, after giving off a branch which anastomoses with the fourth canal. The fourth canal joins the most posterior of the three left side ventral nasobasal canals. The most dorsal pore of the left side arc leads to a highly-branched canal; two of these branches go to the rostral area, and two pass dorsally to open into the floor of the nasal capsule. At several points along this canal there are short branches to the infraorbital sensory canal. Finally, the pore lateral to the arc also leads to the sensory canal. The complicated system of canals described above is not found in any living fish but by comparison with living and fossil dipnoans it may be suggested that they transmitted either maxillary branches of the trigeminal or buccal branches of the facial nerve, or in some cases both.

The bulbous nasal capsules are more completely enclosed in bone than in other actinopterygians. The walls enclosed the ventral, posterior and the medial half of the anterior surface of the capsule, leaving a large fenestra endonarina communis. The latter faces antero-laterally and slightly dorsally, and is covered, except for the fenestra exonarina anterior, by the nasal and narrow strips of the rostral and premaxillary bones. The posterior nasal tube opened laterally between the nasal and the notch in the postorbital wall. The canal for the olfactory nerve opened into the posteromedial wall of the nasal cavity.

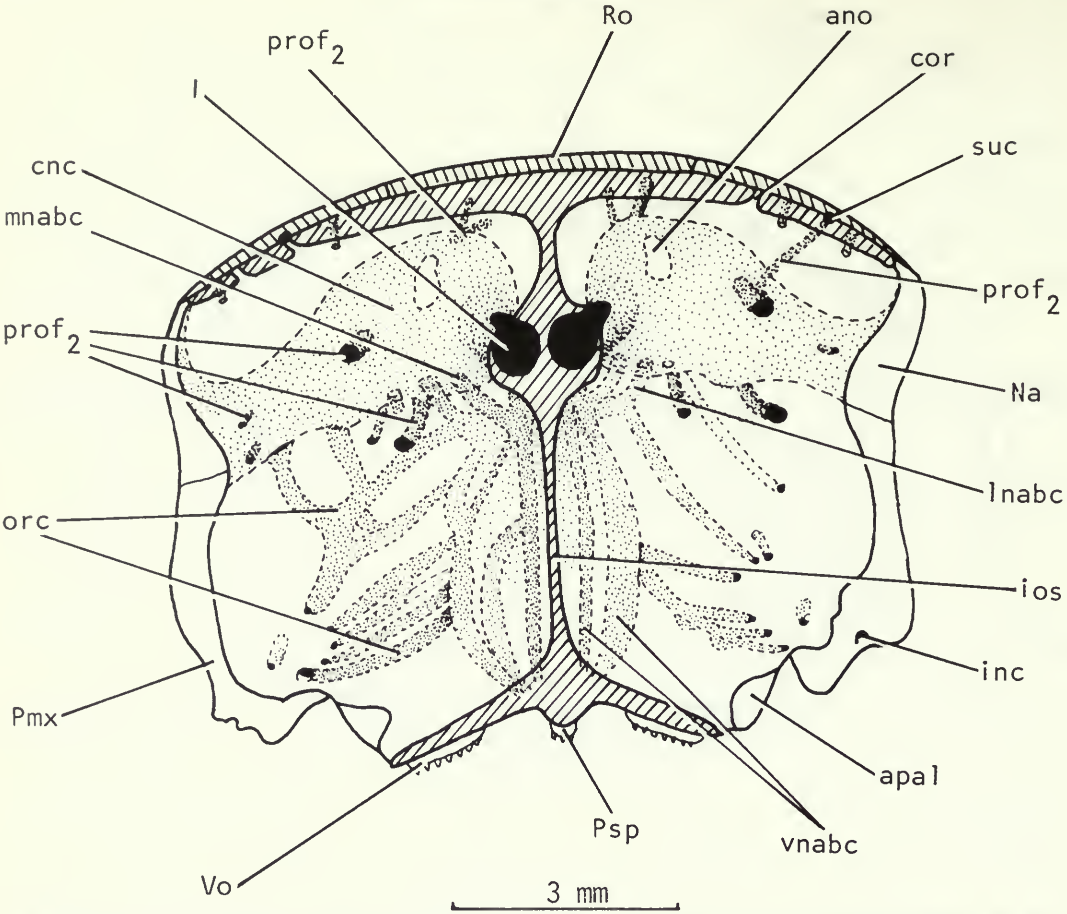

Fig. 39 *Mimia toombsi* Gardiner & Bartram. Braincase and associated dermal bones as if cut transversely through anterior region of orbit; showing postnasal wall in posterior view. Cut surfaces cross-hatched. The intramural canals and cavities lined with perichondral bone are stippled. From BMNH P.56505.

Apart from the pores piercing the posterior wall and floor of the nasal capsule there are two other groups of pores. On the left side two canals, the posterior one branched, run from the roof of the cavity to the rostral above. On the right side there is only one such canal. These canals (prof$_2$, Figs 37, 38, 40) presumably contained twigs of the upper profundus branch which crossed the rear wall of the nasal cavity, as in *Griphognathus* (Miles 1977: fig. 63) and *Porolepis* (Jarvik 1942: fig. 42).

The pores of the second group are larger and pierce the anteroventral corner of the nasal cavity in a row of three (nabc, Fig. 37; mnabc, lnabc, Figs 39, 40), medial to the opening of the dorsal branch of the infraorbital sensory canal (binc, Fig. 37) in the premaxilla. They lead to pores opening beneath the rostral (but not piercing it) and appear to be homologous to the two nasobasal canals (in a similar position) in *Eusthenopteron* (Jarvik 1942: 470). Communicating with the anterior ends of the medial and lateral nasobasal canals in *Mimia* is a further set of canals (three on the left, two on the right) which pass posteroventrally to open by a pair of pores in the roof of the mouth, one on either side of the midline (vnabcf, Figs 38, 41). These are the homologues of the ventral nasobasal canals of *Eusthenopteron* (Jarvik 1942: 470) and presumably transmitted branches of the palatine nerve.

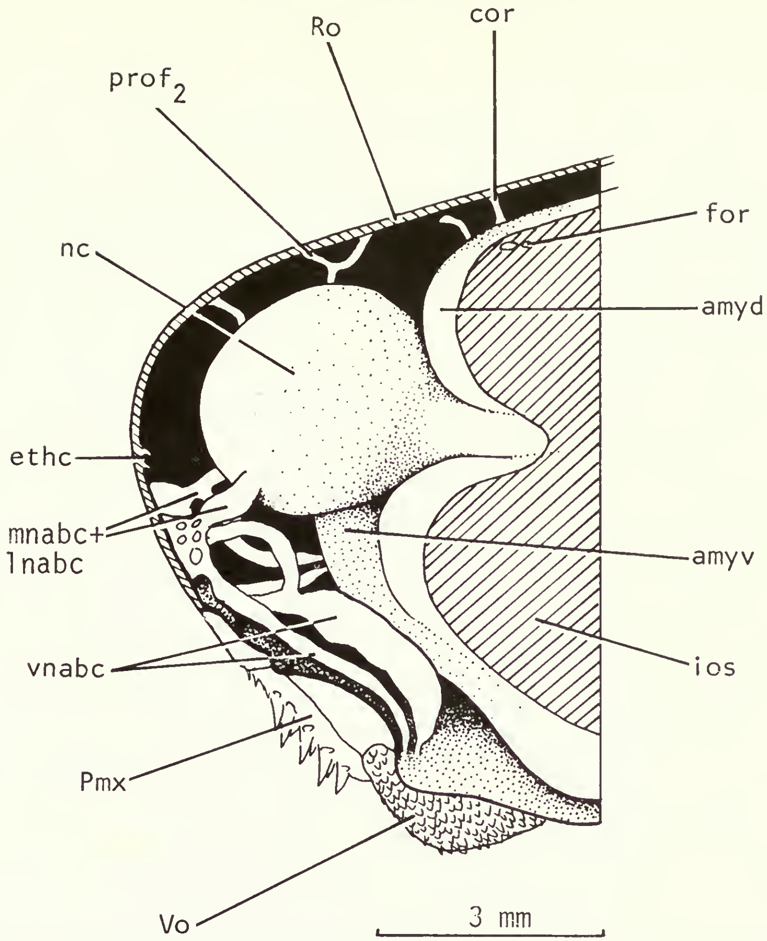

Fig. 40 *Mimia toombsi* Gardiner & Bartram. Ethmoid region of braincase and associated dermal bones in sagittal section, from BMNH P.56505; showing perichondrally lined canals. Sectioned bone cross-hatched.

The ethmoid region of the neurocranium is covered dorsally and anteriorly by a median rostral and paired nasals and premaxillae.

The rostral extends a little over 25% of the length of the skull roof (Figs 41, 101). The rostral is bounded posteriorly by the frontals, which it joins in a serrated suture. The lateral edges of the bone are straight, forming sutures with the nasals except where these two bones are emarginated to form the anterior nostril. At the level of the anterior nostril, the rostral curves sharply ventrally (Fig. 40) and less sharply laterally, thus forming a rounded protruding tip to the snout. The anteroventral edge of the rostral is V-shaped, forming sinuous sutures with the dorsomedial edges of the premaxillae (Fig. 41), which exclude the rostral from the border of the mouth. The external surface of the rostral bears the usual vermiculate pattern of ganoine ridges. The centre of radiation of the bone appears to occur slightly anterior to the mid-point of the line joining the anterior nostrils, at the point of greatest curvature of the bone. The ganoine ridges which extend posteriorly from this point to the frontals are long and parallel (Fig. 42). Anteriorly, the ganoine ridges form an irregular, maze-like radiation. The passage of the ethmoidal commissure is indicated on the external surface of the rostral by an arc of pores (four in BMNH P.56483), which extends through the centre of radiation to points on the lateral part of the suture between the rostral and premaxillae. Internally this sensory canal lay in an open groove limited by two raised ridges of bone (Fig. 42).

The nasals are paired, narrow elongated bones flanking the rostral, and slightly shorter than this bone. The lateral border of the nasal forms a gentle, regular curve limiting the anterodorsal edge of the orbit; this border is not emarginated by the posterior nostril, as it is in many other palaeoniscids. Posteriorly, the nasal forms an oblique suture with the frontal and dermosphenotic. The anterior suture with the premaxilla is transverse and slightly curved. The external surface of the nasal bears long ridges of ganoine orientated along the length of the bone (Fig. 43). These are particularly narrow and closely-spaced near the orbital edge. The ganoine rugae become shorter anteriorly, close to the anterior nostril. The supraorbital sensory canal occupied a groove on the inner surface of the nasal for the first half of its course, but anteriorly was enclosed in a raised tube of bone which ends blindly at the level of the anterior nostril. The passage of the canal is indicated externally by a row of fine pores (five in BMNH P.56483). In many specimens (e.g. BMNH P.56483) the nasal bears a short pit-line anterior to, and in line with, the supraorbital canal; this pit-line probably represents the anterior continuation of the sensory canal, as in *Polypterus*.

The paired premaxillae are flat bones facing anteriorly and slightly laterally and ventrally, and form the anterior edge of the mouth. This edge bears two kinds of teeth. The larger kind forms a row of about ten inner teeth. These are deciduous, leaving large circular scars on the bone; they do not differentiate a sharply-defined enamel (acrodin) cap and match the major teeth on the dentary and maxilla. The smaller teeth, whose equivalents are also found on the last two bones, are exterior to the major teeth, and occur close to the edge of the mouth (Fig. 44). The lateral edge of the premaxillary tooth row gives way to a small area of overlap for the first infraorbital bone (lachyrmal). The infraorbital sensory canal entered this area of the premaxilla. The lateral edge of the premaxilla lies alongside the lateral edge of the postnasal wall of the ethmoid region of the braincase below the posterior nostril; the edge of the premaxilla completes, with the nasal and dermosphenotic, the curve of the dorsal and anterior edge of the orbit. The two premaxillae form a short, straight median suture with each other. The sutures with the rostral and nasal bones are described above.

The ornament of the premaxilla is complex. Along the orbital edge it consists of the usual straight, narrow, parallel rugae and along the oral edge, close to the teeth, it is in the form of ganoine tubercles. Between these two regions extends an area of irregular, vermiculate rugae orientated mainly towards the tip of the snout. The pattern of sensory canal pores is also complex. An irregular line of pores passes from the ventrolateral corner of the bone to the suture with the rostral. This line belongs to the anterior part of the infraorbital sensory canal. Internally this canal was housed in a tube which becomes an open groove in the upper part of the bone (Fig. 44); the tube is pierced by fine pores which transmitted nerves from the buccal and maxillary rami of the facial and trigeminal nerves. A short, dorsal branch of the infraorbital sensory canal, enclosed in bone, opens internally into the nasal cavity before reaching the dorsal edge of the premaxilla. Apart from the pores belonging to the infraorbital sensory canal, there are others which vary in position and distribution from specimen to specimen. Thus in the right premaxilla of BMNH P.56505 these pores are distributed above and below the middle region of the infraorbital canal. The left premaxilla of the same individual has only the ventral pores.

The ethmoid region is partly covered ventrally by an anterior projection of the parasphenoid and by a pair of vomers (Vo, Figs 41, 50, 55). The vomers are small, triangular-shaped ossifications which lie medial to the articular facets for the palatoquadrates and in front of the postnasal wall. A median tongue of the parasphenoid passes between them (Psp, Fig. 50). The vomers are covered by sharply-pointed teeth, larger than those on the parasphenoid.

Moythomasia durgaringa

Unfortunately, no specimen of this species has been found so far in which the ethmoid region is well preserved. Nevertheless the orbital face of the postnasal wall is visible in several specimens. It is very similar to that described in *Mimia*; there is the same dorsolateral gap in the canals for the olfactory nerves (Fig. 7) and there are two anterior myodomes with the lower pair having the

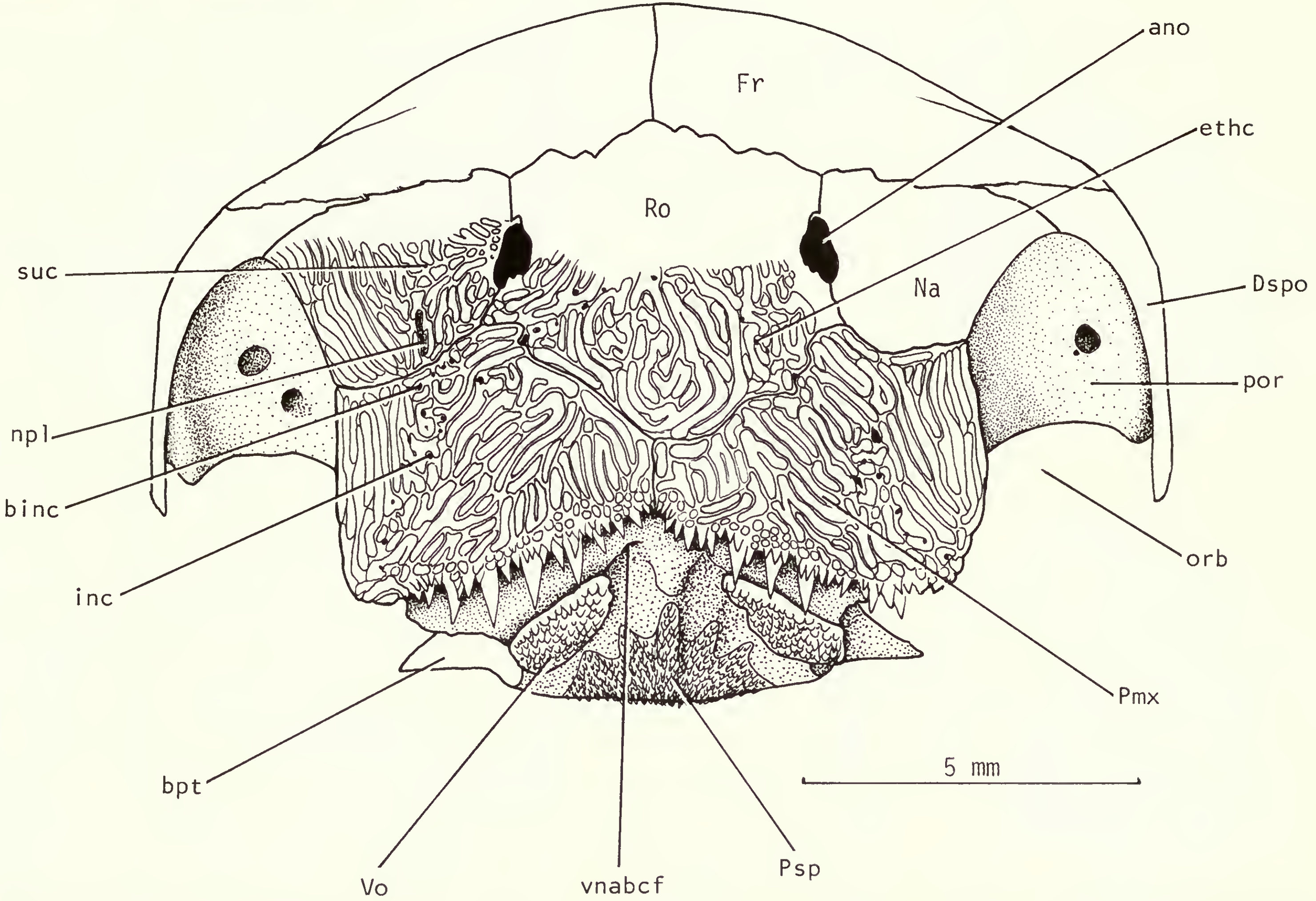
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Fig. 41 *Mimia toombsi* Gardiner & Bartram. Braincase and associated dermal bones in anterior view, based on BMNH P.56505. Ornamentation only partly shown.

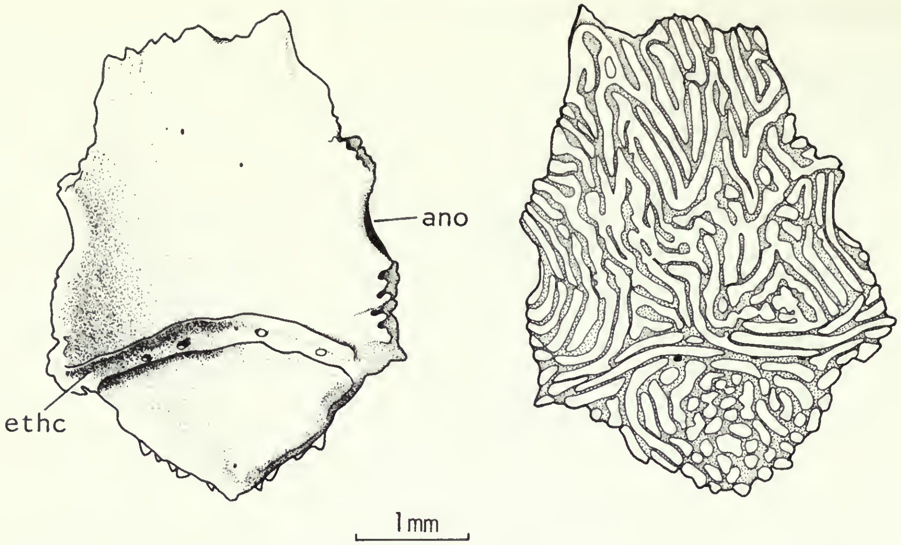
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Fig. 42 *Mimia toombsi* Gardiner & Bartram. Rostral in posterior (left) and anterior views, from BMNH P.56483.

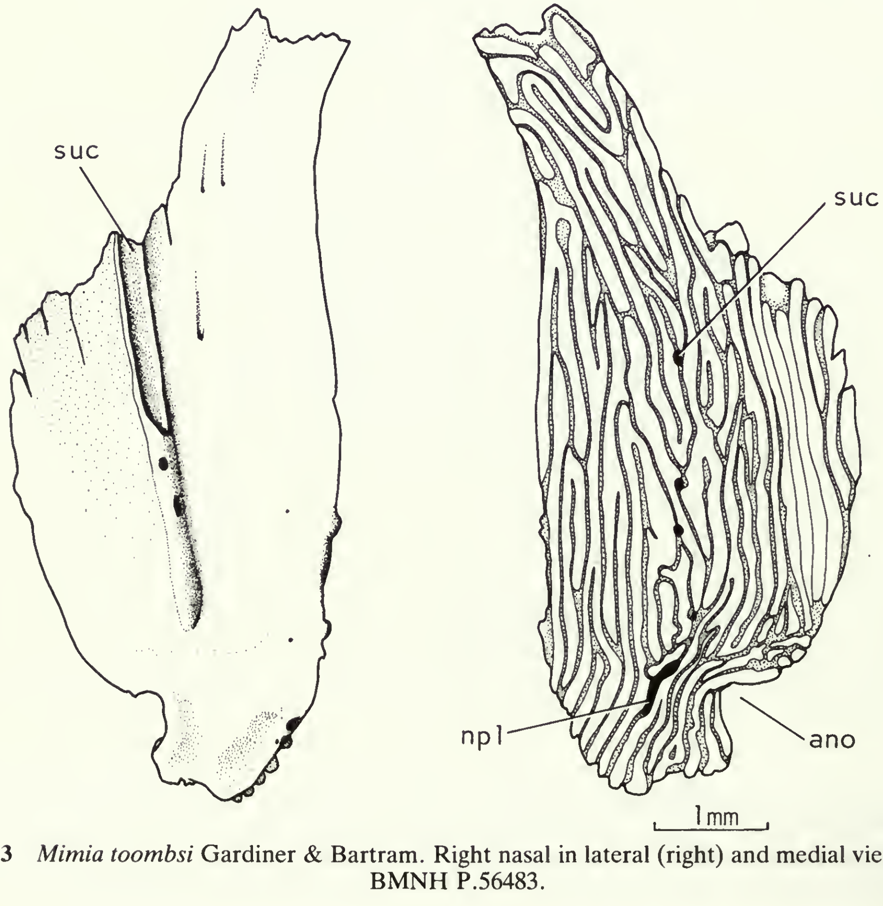
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Fig. 43 *Mimia toombsi* Gardiner & Bartram. Right nasal in lateral (right) and medial views, from BMNH P.56483.

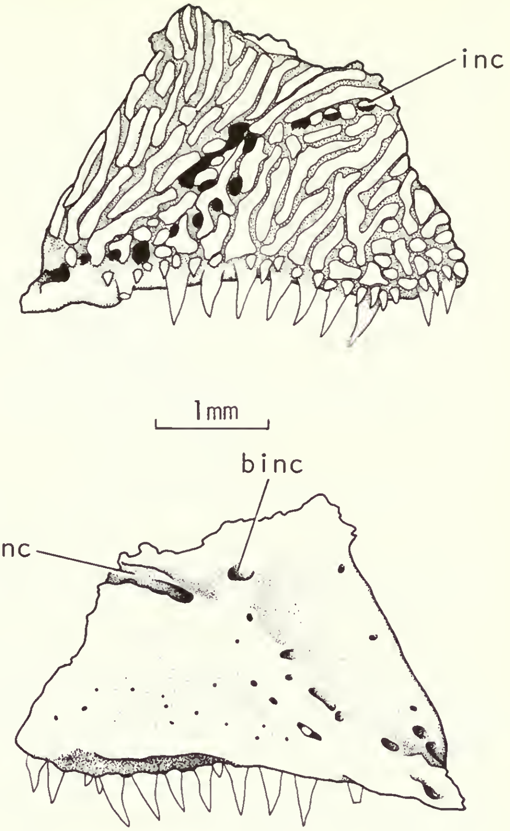

Fig. 44 *Mimia toombsi* Gardiner & Bartram. Right premaxilla in lateral (above) and medial views, from BMNH P.56483.

greater rostral extension. Similarly the articulations for the palatoquadrates occur at the junction of the postnasal wall and suborbital shelf, and the postnasal wall is pierced by a large number of pores. The nasal capsules are bulbous and are enclosed to the same extent as in *Mimia*.

The same dermal bones cover the ethmoid region as in *Mimia*, but their shape and extent are quite different. The rostral extends for over 25% of the length of the skull roof and forms a highly digitate suture with the frontals posteriorly. Behind the anterior nostrils the lateral edges of the rostral are straight and parallel, but at the level of the anterior nostrils, where the bone curves sharply ventrally, the lateral edges flare outwards and then converge, so that the anteroventral edge of the rostral is V-shaped (Figs 45, 48). Unlike *Mimia*, the rostral in *Moythomasia* separates the two premaxillae and takes part in the border of the mouth. The ornamentation of the rostral consists of very stout tubercles and ridges of ganoine, which for the most part have fused into an irregular maze-like configuration. The centre of radiation is considerably anterior to the anterior nostrils and the ethmoid commissural sensory canal passed through it. Internally this canal was housed in a tube, pierced by two fine pores (Fig. 45) which presumably transmitted branches of the buccal and maxillary nerves. On the ventral margin of the bone the ganoine tubercles are pointed and give way to one (Fig. 48) or two (Fig. 45) teeth which correspond to the smaller teeth on the premaxillae, maxillae and dentaries, external to the major, replaceable teeth.

The nasals are paired, narrow bones and the sutures between them and the rostral are straight except where they are interrupted by the notch for the anterior nostril. The lateral border of the nasal is emarginated by a much larger notch for the posterior nostril. Posteriorly, the nasal forms an oblique suture with the frontal and dermosphenotic, and ventrally it overlaps the premaxilla for a short distance (Fig. 48). Anteroventrally, a little beyond the notch for the anterior nostril, the nasal loses contact with the rostral altogether and a large foramen is formed between the rostral, nasal and premaxilla. The external surface of the nasal bears massive fused tubercles and ridges of ganoine which latererally, near the orbital edge, are orientated along the length of the bone. The supraorbital sensory canal extended in a groove on the inner surface of the nasal and terminated at the level of the dorsal margin of the anterior nostril. The passage of the canal is indicated externally by a row of eight pores in BMNH P.53255 (Fig. 46). Lateral to and parallel with this sensory canal is an elongate foramen (p, Fig. 48). In other specimens (Fig. 46) this foramen is the same size as the sensory canal pores.

The flat, stout premaxillae face anterolaterally, and ventrally bear two kinds of teeth. There are never more than four of the deciduous larger kind, which have sharply-defined enamel caps (acrodin). The smaller, pointed teeth form an external row of some 15–20 (Fig. 48). Anteriorly the premaxilla is in sutural contact with the rostral but dorsally the suture gives way to a small area of overlap for the nasal. Posteriorly, above the tooth row, the posterior margin has a more extensive overlap area for the first infraorbital (lachrymal). The lateral edge of the premaxilla lies alongside the lateral edge of the postnasal wall and forms the lower margin to the posterior nostril.

The ornamentation on the premaxilla is similar to that on the rostral, with stout striae of ganoine dorsally and rounded tubercles ventrally. Internally the infraorbital sensory canal was housed for the most part in an open gutter, though the dorsal branch which opens short of the dorsal edge of the premaxilla was enclosed in a tube. The course of the infraorbital sensory canal is marked externally by a line of up to twelve pores which in some specimens are in the form of slits. Below the middle region of the infraorbital canal is a further series of four pores, which lead into a short canal within the bone. Internally this canal is pierced by three pores (p, Fig. 47).

The paired vomers are covered by sharply-pointed teeth, the posterior row of which is much enlarged (Gardiner & Bartram 1977: fig. 7). The vomers are widely separated, irregular in outline and lie medial to the articulation facets for the palatoquadrates (Fig. 7).

Ethmoid region: discussion

1. *Anterior myodome.* Two pairs of anterior myodomes appear to be present in most palaeoniscids (*Mimia, Moythomasia, Kentuckia, Pteronisculus, Boreosomus*). In the palaeoniscid *Kansasiella* (Poplin 1974: fig. 18), however, the ventral anterior myodome is median. In the pholidopleurid *Australosomus* there is a single, large paired anterior myodome ventral

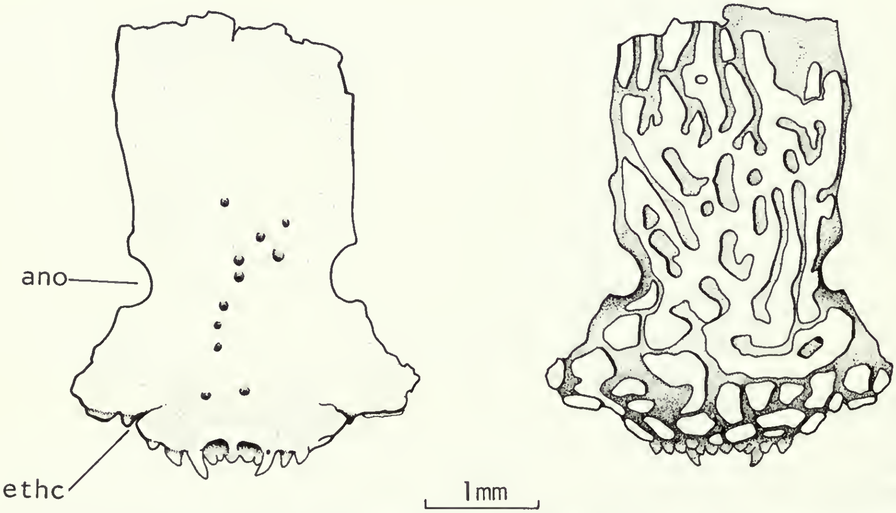

Fig. 45 *Moythomasia durgaringa* Gardiner & Bartram. Rostral in posterior (left) and anterior views, from BMNH P.53255.

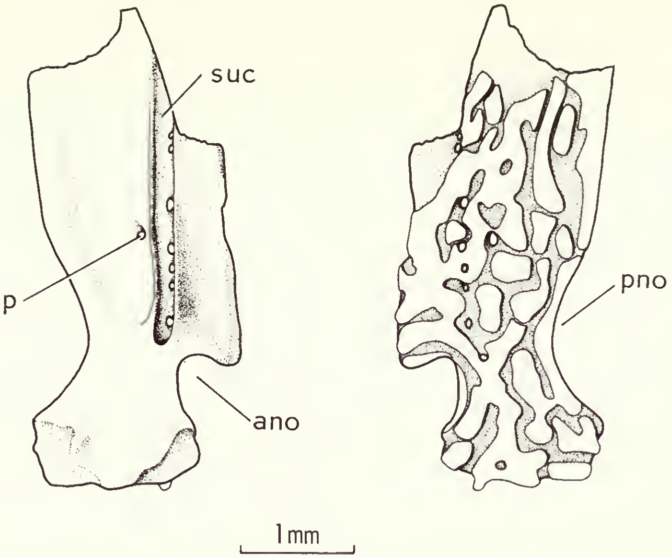

Fig. 46 *Moythomasia durgaringa* Gardiner & Bartram. Left nasal in lateral (right) and medial views, from BMNH P.53255.

to the olfactory nerve canal (Nielsen 1949: fig. 13). Two pairs of rather shallower anterior myodomes are present in *Saurichthys*, parasemionotids, *Macrepistus* (Schaeffer 1971: fig. 6) and *Dapedium*, and as in palaeoniscids the upper pair lie dorsal to the olfactory nerve canal and often communicate with one another through an interorbital fenestra. In some caturids (*Caturus, Heterolepidotus, 'Aspidorhynchus'*), however, the dorsal myodome is obscured by an enlarged interorbital fenestra (Patterson 1975: fig. 102). In *Amia* both oblique muscles, together with a vein, pass through a large orbitonasal canal into the olfactory nerve canal and are attached to its floor.

In *Pachycormus* (Patterson 1975: 516) there is no ventral anterior myodome, and in this it resembles pholidophorids and Recent teleosts where there is a median, dorsal anterior

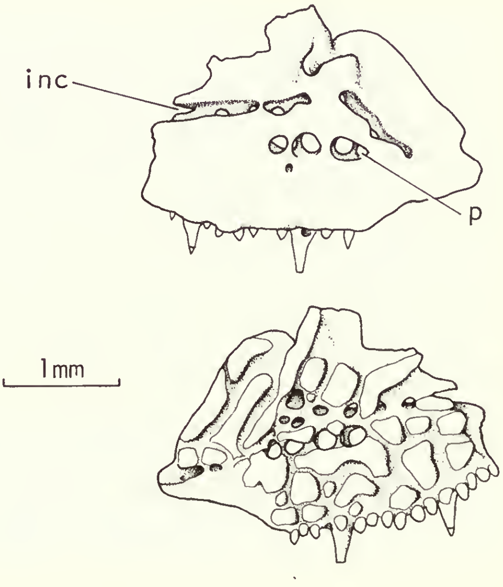

Fig. 47 *Moythomasia durgaringa* Gardiner & Bartram. Right premaxilla in medial (above) and lateral views, from BMNH P.53255.

myodome and where both pairs of oblique muscles enter the foramen olfactorium evehens; this is a specialization.

There is no anterior myodome in living chondrosteans or *Lepisosteus*; the oblique muscles originate separately in the former but together in the latter. In *Polypterus* the two muscles are separated as in chondrosteans and dipnoans, but the superior oblique muscle enters the funnel-like opening of the profundus canal where it attaches to the medial wall.

In *Nesides* and *Euporosteus* (Jarvik 1942: fig. 75A, B) there is said to be a single small myodome ventral to the olfactory nerve, similar to that in *Australosomus*, except that through it also ran the orbitonasal artery. In *Diplocercides* (specimen figured by Stensiö, 1922: pl. 3, fig. 1) there are two pairs of shallow ventral myodomes, and these depressions are in a position homologous to the origins of the superior and inferior oblique muscles in *Latimeria*, although in *Latimeria* myodomes are absent. The condition in dipnoans is less easy to interpret, but in larval *Neoceratodus* the superior oblique muscle originates in the upper anteromedial corner of the orbit, whereas the inferior oblique arises near the bottom corner. In adult *Neoceratodus* there are no anterior myodomes and Miles (1977) also failed to find any such structures in the Gogo dipnoans.

In the rhipidistian *Eusthenopteron* (Jarvik 1942: figs 49, 50, fo.m.obl), very shallow paired ventral pits have been described in the postnasal wall, which according to Jarvik (1942: 437) were probably the place of origin of the oblique muscles. No such depressions have so far been described in any other rhipidistian (*Ectosteorhachis, Rhizodopsis, Porolepis, Holoptychius, Youngolepis*); in *Glyptolepis* sp. (BMNH P.47838), however, there are two pairs of shallow ventral myodomes below the profundus canal, in a position homologous to the paired depressions in *Diplocercides*. No myodomes have been described in chondrichthyans but depressions have been noted in the perichondral lining of the front of the orbit in certain placoderms (*Brindabellaspis*, Young 1980: fig. 10), which presumably served as points of origin for individual muscles. A corresponding anteroventral depression in the floor of the orbit of *Macropetalichthys* (Stensiö 1963*b*: fig. 32) has been attributed to the inferior oblique muscle.

From this evidence we may conclude that anterior myodomes, like posterior myodomes, were primitively absent in gnathostomes and osteichthyans. Anterior myodomes have been independently acquired in actinopterygians, actinistians and some rhipidistians. In actinopterygians the anterior myodome typically consists of two pairs of shallow depressions, one pair above and the other below the olfactory nerve canal, whereas in actinistians and rhipidistians the two pairs of depressions are both below the olfactory nerve canal, in the floor of the postnasal wall.

2. *Postnasal wall and nasal capsule*. The ethmoid region of *Mimia toombsi* is traversed by a greater number of canals than in any other osteichthyan and the number of pores piercing the postnasal wall is correspondingly high. The dorsal group of canals (4–7) in the postnasal wall are presumed to have served for branches of the profundus nerve.

The ventral group of canals (5–8) pierce the ventrolateral corner of the postnasal wall (orc, Figs 37–40). The most lateral of these canals communicates with the infraorbital sensory canal and thus must have transmitted the buccal branch of the facial nerve. It is impossible to decide whether the remainder of these canals transmitted maxillary or buccal nerve branches or both. Several of these dorsal and ventral canals (orc, Fig. 39) communicate with the nasobasal canals (mnabc, lnabc, Fig. 39), which run from the nasal cavity to the rostral area and there communicate with a set of ventral nasobasal canals (vnabc, Figs 39, 40). Similar nasobasal canals are found in the floor and anterior wall of the nasal capsule of *Eusthenopteron* (Jarvik 1942: fig. 57), *Glyptolepis* (Jarvik 1972), *Youngolepis* (Chang 1982: fig. 14) and *Griphognathus* (Miles 1977: fig. 62(a), prog.V, V_2) and must be presumed to be a primitive feature of osteichthyans. In *Eusthenopteron* and *Glyptolepis* Jarvik (1942, 1972) considered that these nasobasal canals transmitted branches of the profundus nerve and that the palatonasal canal of *Eusthenopteron* served for a branch of the maxillary nerve. Rosen *et al.* (1981: 192), however, considered that the nasobasal canals in *Eusthenopteron* transmitted the truncus infraorbitalis and accompanying vessels. Miles (1977: 130) decided that in *Griphognathus* the dorsomedial of the two nasobasal canals carried a ventral division of the profundus nerve, whereas the lateral canal transmitted the maxillary nerve.

Thus we may conclude that the nasobasal canals transmitted maxillary and buccal nerve branches as well as branches of the profundus nerve.

The olfactory organ in fishes is a blind sac, with a single anterolateral or ventrolateral aperture. This aperture is varyingly subdivided by flaps or more extensive tissue barriers into incurrent and excurrent openings. Each olfactory organ is surrounded by cartilage or bone apart from a single anterolateral aperture which serves for both incurrent and excurrent streams. This nasal capsule is developed in continuity with the front end of the trabeculae; a median septum nasi separates the right from the left capsule, the floor of the capsule is termed the solum nasi and the roof the tectum. This is essentially the condition in *Chlamydoselachus* and *Polypterus*.

Primitively in osteichthyans the postnasal wall is ossified by the lateral ethmoids (*Polypterus, Latimeria, Acipenser, Amia* and teleosts), but the only living fishes with any endoskeletal ossification anterior to the postnasal wall are *Amia*, teleosts and *Latimeria*. However, the nasal capsule is more or less completely perichondrally ossified in *Mimia, Moythomasia* and *Europorosteus* (Jarvik 1942: 556) and in *Eusthenopteron* (Jarvik 1972: fig. 66D) and *Griphognathus* there is also some endochondral bone present. In *Mimia* and *Moythomasia* the ethmoid region is a shell of thin perichondral bone with all the canals for nerves and blood vessels also surrounded by tubes of perichondral bone. Consequently it is difficult to recognize individual ossification centres in this region. Nevertheless, it would appear that paired lateral ethmoids were primitively developed in the postnasal wall of osteichthyans because paired lateral ethmoids are found in *Polypterus, Acipenser, Birgeria, Perleidus, Lepidotes, Caturus, Macrepistius, Amia*, pachycormids, Recent teleosts, *Macropoma* and *Latimeria* (Patterson 1975: 499).

In *Amia*, pholidophorids, *Hypsocormus* and Recent teleosts there are additional endoskeletal ossifications. Paired pre-ethmoids occur in *Amia* and *Hypsocormus*, a median supraethmoid, ventral ethmoid and anterior myodome bones are found in pholidophorids and up to five ossifications are present in some teleosts, including a median supraethmoid, ventral ethmoid and anterior myodome bones and paired capsular ethmoid bones. As Patterson (1975: 502) concluded, there is good evidence that the region anterior to the lateral ethmoids is a new formation in advanced actinopterygians. In other words there has been an increase in the number of ossification centres. From this I conclude that the primitive osteichthyan possessed one pair of ossifications in the ethmoid region, the lateral ethmoids, and that each olfactory organ was completely surrounded by bone apart from a lateral aperture.

3. *Dermal bones of the snout*. Primitively the roof of the nasal capsule in actinopterygians is covered by a broad, shield-like rostral, bordered by the frontals behind and the nasals laterally. The rostral contains a portion of the ethmoid commissure. This is essentially the condition in *Polypterus* and palaeoniscids. In most previous descriptions of palaeoniscids (e.g. Aldinger 1937; Moy-Thomas & Dyne 1938; Nielsen 1942, 1949; Gardiner 1963, 1967; Jessen 1968) the rostral is mistakenly called the postrostral, but it is now clear that it is penetrated by the ethmoid commissure in almost all instances. Re-examination of *Cheirolepis* (Fig. 49) has convinced me that the rostral is a single ossification (e.g. BMNH P.60533, P.4051a; GSM 88873; RSM 1973.12.150) and there is little evidence for considering it to be comprised of several ossifications as Gardiner (1963) and Pearson & Westoll (1979) have suggested. The evidence for a lateral postrostral in *Cheirolepis canadensis* (Pearson & Westoll 1979: fig. 3d, h) rests on the interpretation of a single specimen (BMNH P.6815). In my estimation this lateral postrostral is more reasonably interpreted as the rostral.

A similar shield-like rostral is also met with in pholidophorids (Patterson 1975: 497), perleidids, redfieldiids, ptycholepids and *Dapedium*, but in *Pachycormus* (Patterson 1975: 511) the large median rostral has fused with the underlying, toothed, lateral dermethmoids. In parasemionotids (Patterson 1975: fig. 137), caturids (*Caturus, Furo, Heterolepidotus, Osteorachis*), amiids, many semionotids (*Acentrophorus, Lepidotes*) and *Lepisosteus* (Patterson 1975: figs 135, 136) the median rostral is reduced to little more than a tube around the

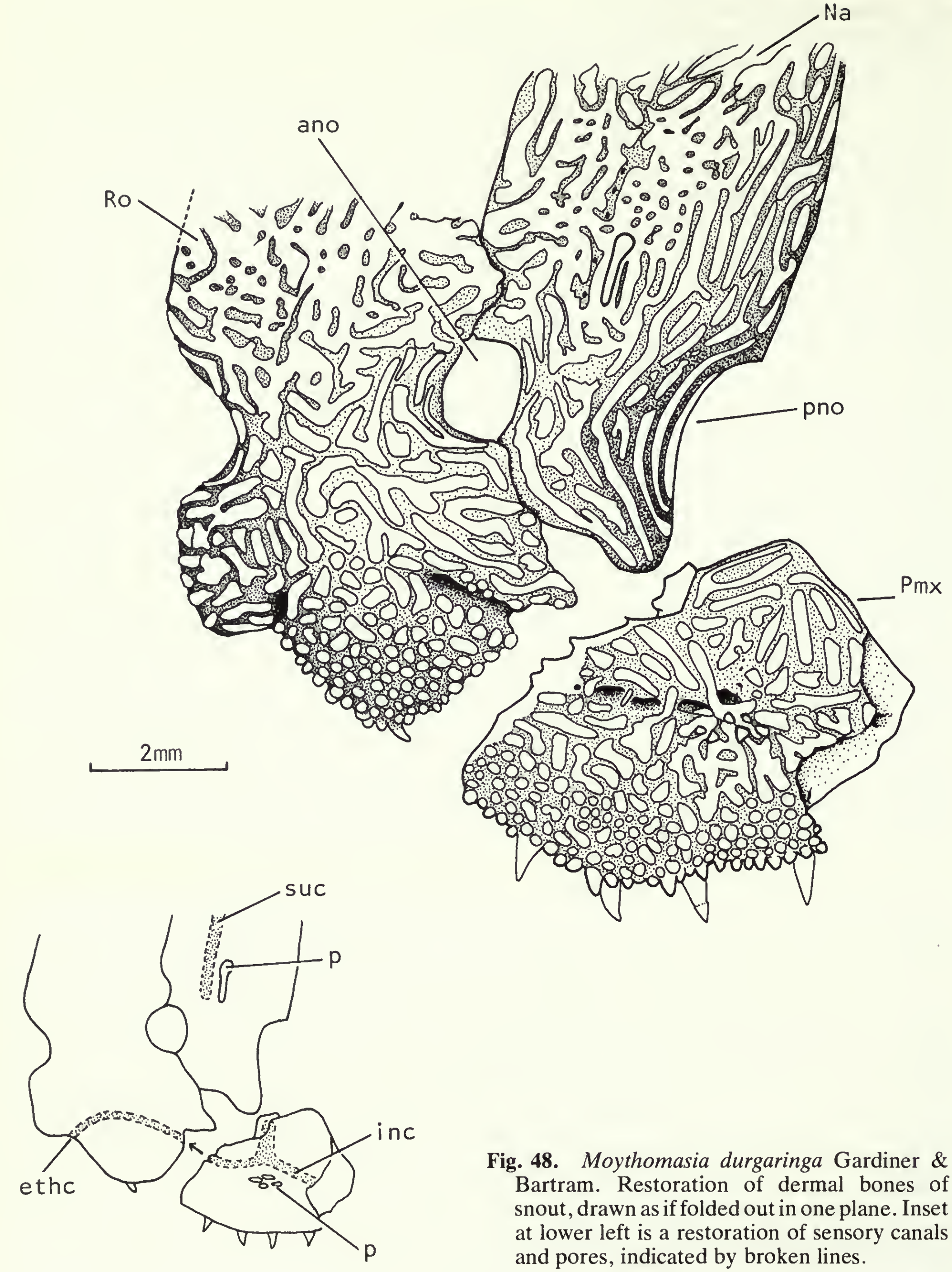
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Fig. 48. *Moythomasia durgaringa* Gardiner & Bartram. Restoration of dermal bones of snout, drawn as if folded out in one plane. Inset at lower left is a restoration of sensory canals and pores, indicated by broken lines.

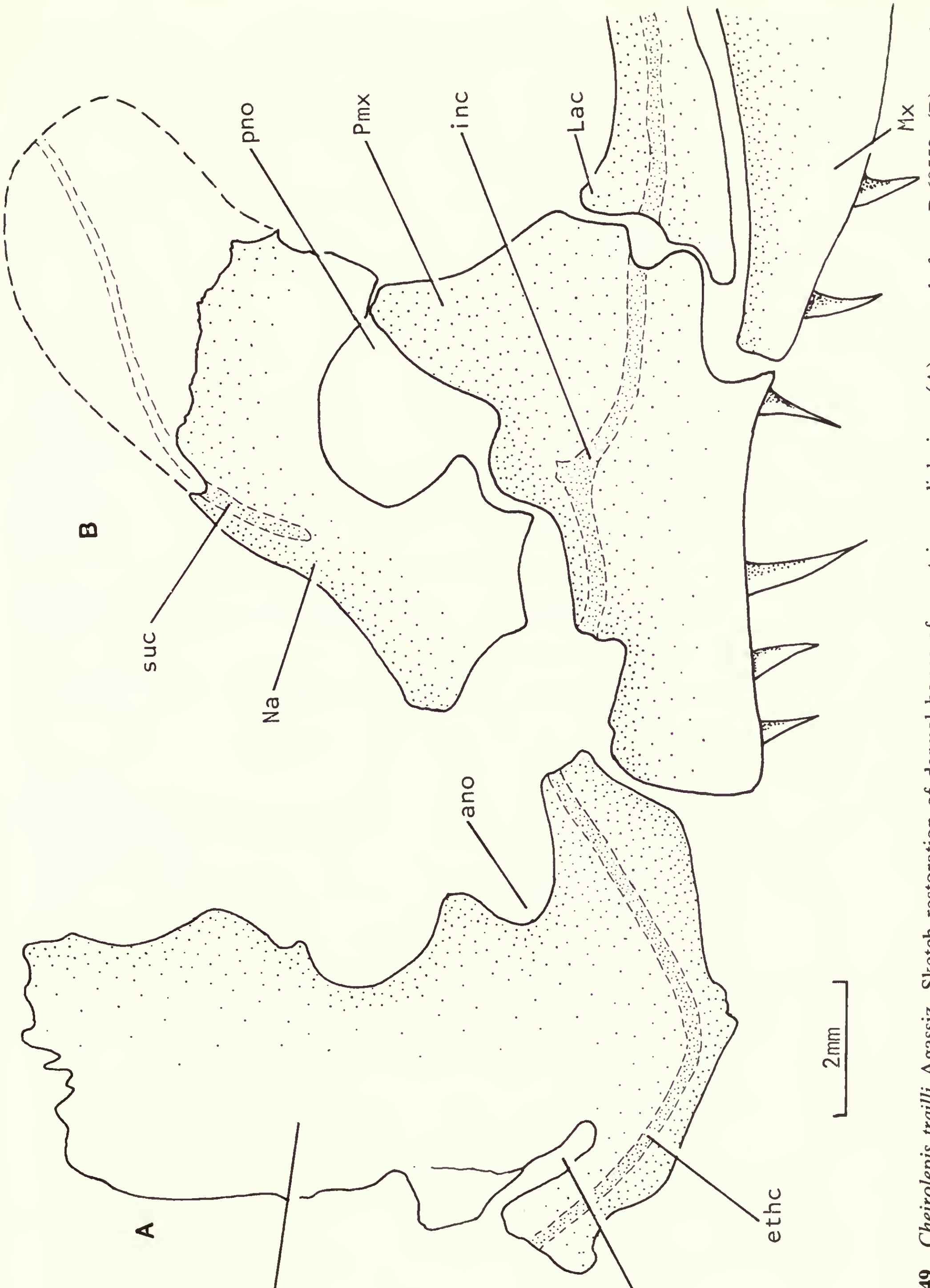
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Fig. 49 *Cheirolepis traillii* Agassiz. Sketch restoration of dermal bones of snout in medial view. (A), rostral, from P.60553; (B), nasal, premaxilla, lachrymal and maxilla from P.53903*a*.

ethmoid commissure with the nasals meeting in the mid-line behind it. In teleosts, where the ethmoid commissure remains bone-enclosed (e.g. leptolepids, *Megalops, Elops*), the tube-like rostral is fused with the underlying dermethmoid as in *Pachycormus* (Patterson 1975: 511).

A median rostral is also found in *Holoptychius* (Jarvik 1972: figs 35, 36) where it is so small that it only just embraces the ethmoid commissure. The rostral of actinopterygians may have captured the middle part of the ethmoid commissure as Patterson (1975: 512) suggests, or conversely it may have been primitively associated with it. Support for the latter point of view is afforded by its presence in the rostrals of actinopterygians and *Holoptychius*, and for the former by the condition in actinisitians, where in fossil forms (*Laugia, Rhabdoderma, Macropoma*) the ethmoid commissure is contained within the premaxillae as in some rhipidistians (*Eusthenopteron* Jarvik 1942; *Osteolepis* Jarvik 1948; *Megalichthys* Thomson 1964). In *Latimeria* the commissure is separate from the underlying premaxillae and bears four short bones along its length. An ethmoid commissure wholly contained within the premaxilla is found in early actinistians and osteolepiforms, and this is believed to be primitive. Conversely a shield-like rostral is considered synapomorphous for actinopterygians.

The remaining portion of the snout was primitively covered in actinopterygians by the paired, toothed premaxillae which contain the characteristic triradiate anterior portion of the infraorbital sensory canal and the greater part of the ethmoid commissure. The premaxilla in early actinopterygians has often been termed the rostro-premaxillo-antorbital because the premaxilla and antorbital of higher actinopterygians are believed to result from its subdivision (Gardiner 1963). However, it is better to regard this bone in early actinopterygians as the premaxilla as it is homologous with that bone in rhipidistians where it also bears replacement teeth and the triradiate portion of the infraorbital sensory canal.

A canal-bearing premaxilla is found in all Devonian palaeoniscids, ptycholepids and *Polypterus*, but in perleidids, parasemionotids, caturids, amiids, semionotids, pachycormids, pholidophorids and Recent teleosts the premaxillary and antorbital (canal-bearing) components are separate.

The nasal is single in actinopterygians with the exception of *Polyodon* and *Polypterus* where there are three. The nasal in *Cheirolepis* (BMNH P.65527, P.65528, P.4050) is very similar in shape to that of *Mimia* and there is little evidence to suppose it is composed of more than one ossification.

Tetrapods, like most actinopterygians, have a single pair of nasals, but elsewhere in osteichthyans the number is higher. In primitive actinistians (*Diplocercides* Stensiö 1937) there are five pairs of nasals, and some dipnoans (*Soederberghia* Lehman 1959) have as many as eight. In osteolepids, *Eusthenopteron* (Jarvik 1948: fig. 16) has three, *Megalichthys* and *Osteolepis* six, while the porolepid *Holoptychius* (Jarvik 1972: figs 35, 36) usually has five nasals. Primitively in osteichthyans there were probably four or more nasals. In primitive actinopterygians there was one.

In a previous publication (Gardiner 1963) I assumed that the antorbital branch of the infraorbital sensory canal primitively anastomosed with the terminal portion of the supraorbital canal between the nostrils in actinopterygians (see however Jollie 1969). The supraorbital canal does anastomose with the infraorbital canal in *Lepisosteus, Amia, Latimeria*, porolepids and osteolepids, but in dipnoans, *Cheirolepis, Mimia, Moythomasia, Polypterus*, chondrosteans and teleosts (Nybelin 1967) it does not.

The primitive osteichthyan condition probably lacks such an anastomosis. In the primitive actinopterygian the supraorbital canal passed between the nostrils as in chondrosteans, *Polypterus, Lepisosteus* and *Amia*. In *Latimeria* the supraorbital canal joins the infraorbital both in front of and between the nostrils, whereas in osteolepids and porolepids the supraorbital and infraorbital canals anastomose in front of the nostrils. In chondrichthyans and some placoderms the anastomosis of the two canals is behind the nostrils. In fossil dipnoans such as *Holodipterus* (BMNH P.52566) the ethmoid commissure connects the two supraorbital canals rather than the two infraorbital canals as it does in actinopterygians, chondrichthyans and some placoderms. The former condition must be regarded as secondary and in part due to the interruption of the infraorbital sensory canal by the choana in dipnoans and primitive tetrapods.

In osteichthyans there is a further series of bones associated with the roof of the nasal region, the internasals or postrostrals. These are anamestic bones, variable in number and arrangement. In actinopterygians these elements occur only in long-snouted forms such as *Acipenser* (where there are more than twelve internasals), *Polyodon, Chondrosteus* and *Saurichthys* (where there is a single pair of extremely long bones). In actinistians the internasals form a median series of five or more in *Diplocercides* (Stensiö 1937), two or more in *Latimeria*, and one in *Rhabdoderma* (Forey 1981). In dipnoans there may be a single median internasal, as in *Fleurantia* (Graham-Smith & Westoll 1937), *Ceratodus* and *Neoceratodus*, long paired internasals, as in *Griphognathus* (Miles 1977: fig. 111), *Holodipterus* and *Scaumenacia* (Holmgren & Stensiö 1936), or an irregular series, as in *Dipnorhynchus, Uranolophus* (Denison 1968, 1969) and *Chirodipterus* (Miles 1977). In osteolepids, *Megalichthys* (Thomson 1964) has a single internasal, *Osteolepis* (Jarvik 1948) two median internasals, *Panderichthys* (Vorobjeva 1973) four and *Eusthenopteron* one large median internasal and five smaller anterior ones. The porolepid *Holoptychius* (Jarvik 1972: fig. 35) has an irregular series of eight to fourteen internasals. A small median internasal is present in *Ichthyostega* (Jarvik 1952) and loxommatids, but in no other tetrapod. From this we may conclude that internasals are primitively present in sarcopterygians but absent in actinopterygians.

Finally, there is one further series of bones associated with the nasal region in osteichthyans, the tectals, which are not canal-bearing and form a series lateral to the nasals and dorsal to the nostrils. Tectals are present in osteolepids (*Eusthenopteron, Osteolepis*), actinistians (*Rhabdoderma, Latimeria*), porolepids (*Holoptychius*) and dipnoans (*Dipnorhynchus, Chirodipterus*), but absent in actinopterygians. Thus I conclude that tectals are a synapomorphy of sarcopterygians.

Parasphenoid and associated toothplates

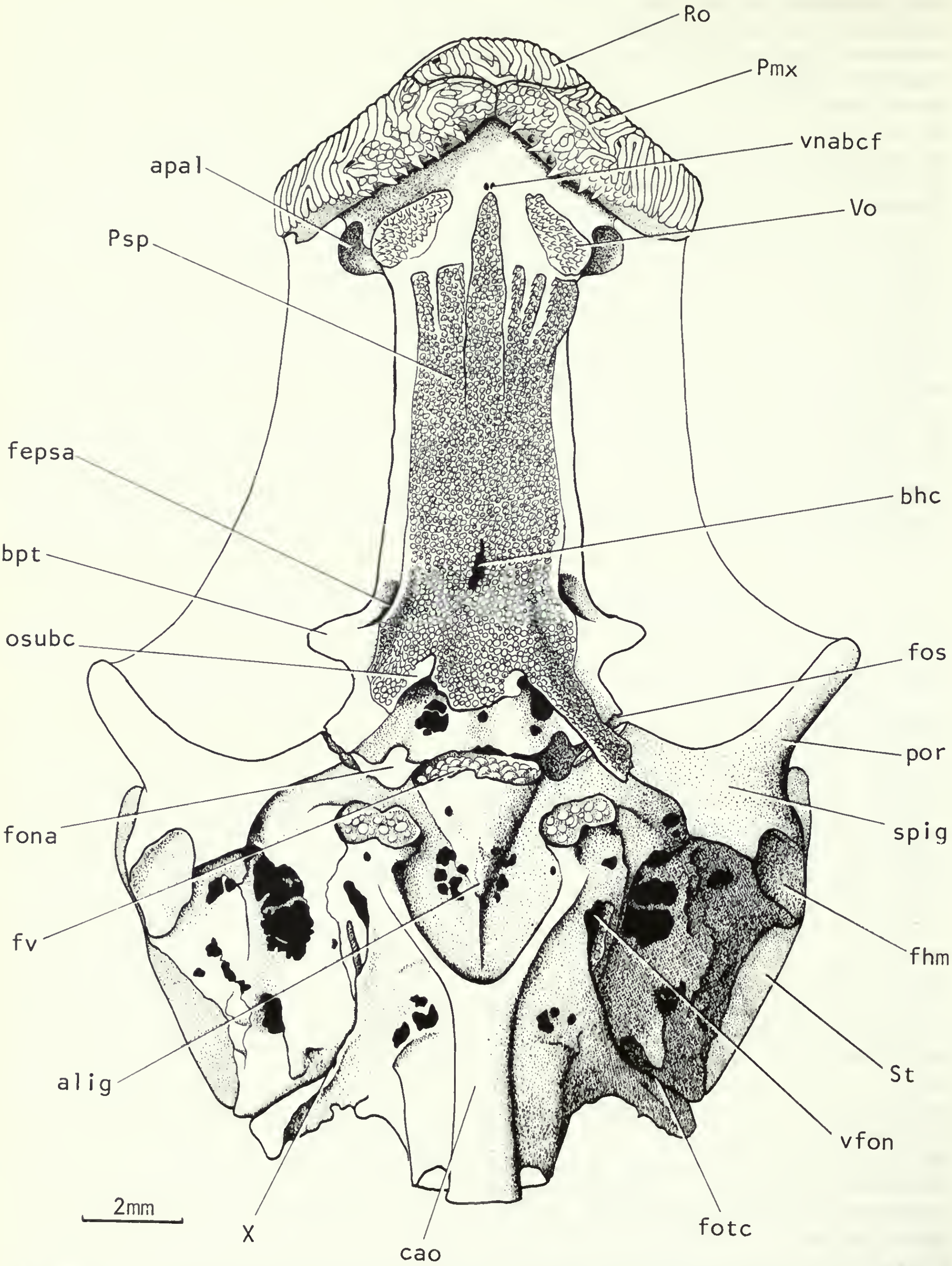
The parasphenoid is without a stalk (posterior elongation below the otic region) in the Gogo palaeoniscids and this is considered primitive for osteichthyans and placoderms.

Mimia toombsi

The parasphenoid is shown in lateral view in Fig. 13 and in ventral view in Fig. 50. It is a broad bone, of roughly rectangular shape, with a pectinate anterior margin. A median tongue of bone extends from this anterior margin to terminate between the vomers posterior to the paired openings of the ventral nasobasal canals. Behind the basipterygoid process the parasphenoid is produced into a short, posterolaterally-directed arm which passes up towards the oticosphenoid fissure. Occasionally, as in BMNH P.53247 (Fig. 50), one of these arms may project back below and behind the spiracular canal, but this projection is not an ascending process in the strict sense (Gardiner & Bartram 1977: 231). A short median posterior extension ends at the level of the ventral fissure or occasionally a short distance in front of it. Posteriorly this extension is not applied to the basisphenoid and in this respect it is similar to that of *Australosomus* (Nielsen 1949: fig. 26). The buccal surface is completely covered by teeth, apart from two notches which delimit the posterolateral arms from the medial portion. The smooth areas around these notches (osubc, Fig. 50) probably mark the points of insertion of the subcephalic muscles (Nelson 1970*a*: 468). On the dorsal surface at the level of the basipterygoid process the parasphenoid is produced into a small cup around the wide bucco-hypophysial canal (see *Moythomasia*, bhc, Fig. 52). The bucco-hypophysial canal passes through the centre of ossification. From the ventral opening of the bucco-hypophysial canal paired spiracular grooves (Fig. 50; see also *Moythomasia*, spig, Fig. 51) pass back towards the oticosphenoid fissure.

There is no dermal basipterygoid process (anterior ascending process) and in this respect *Mimia* resembles *Cheirolepis*. The efferent pseudobranchial artery passed in between the parasphenoid and the basisphenoid (fepsa, Fig. 50).

A paired toothplate is associated with the parasphenoid in *Mimia*. It is an elongate, ovoid plate, rounded anteriorly but more pointed posteriorly, which fits between the edge of the parasphenoid and the entopterygoid, overlapping the latter. This paired bone (Av, Fig. 53) is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St
vfon
2mm
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cao
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Fig. 50 *Mimia toombsi* Gardiner & Bartram. Restoration of braincase in ventral view, based on BMNH P.56496 and P.53247. From Gardiner & Bartram (1977).

shallowly concave dorsally and its entire oral surface is covered with closely-set, small teeth similar to those on the parasphenoid. It covers the toothless zone between the lateral edge of the parasphenoid and the adjoining part of the entopterygoid. It stretches from the foramen for the efferent pseudobranchial artery to just behind the vomer (Vo, Fig. 50). I will call it an accessory vomerine toothplate. An almost identical pair of toothplates occurs in *Moythomasia* and *Pteronisculus* (Nielsen 1942: fig. 34, Vo); a narrower, smaller pair has been described in *Australosomus* (Nielsen 1949: fig. 26). It is probable that these toothplates are widespread in the palaeoniscids.

Moythomasia durgaringa

The parasphenoid (Figs 7, 51, 52) is more extensive than in *Mimia*. Anteriorly it reaches the lateral margins of the basisphenoid and posteriorly not only extends to the level of the ventral fissures but also bears rudimentary ascending processes (asp, Fig. 7). Its toothed area, however, is less extensive than in *Mimia* and in front of the bucco-hypophysial canal only the central third of the bone is toothed. Anteriorly the median tongue of bone is little longer than the paired lateral ones and terminates at the level of the posterior margins of the vomers.

Behind the foramen for the efferent pseudobranchial artery the parasphenoid of one specimen (BMNH P.53221) continues out for a short distance onto the basipterygoid process on one side only, but this can hardly be considered to be a true dermal basipterygoid process (anterior ascending process). Posteriorly the posterolateral arm extends up onto the corner of the prootic forming an ascending process (or posterior ascending process) which terminates level with the bottom of the jugular canal. The ascending process, like the rest of the area behind the basipterygoid processes, is covered with teeth which are never as large as those in front of the bucco-hypophysial canal. The spiracular groove (spig, Fig. 51) which passes back on the oral surface from the bucco-hypophysial canal extends onto the ascending process. Posteriorly the parasphenoid is spear-shaped, with a shallow, smooth ledge forming the hindmost margin. Between this spear-shaped portion and the ascending process is a distinct notch (gic, Fig. 51). The outer border of this notch is smooth (osubc) and presumably served for the insertion of the subcephalic muscle.

Immediately behind the parasphenoid in the roof of the mouth there is a pair of parotic toothplates (Gardiner & Bartram 1977: 240). These plates fill the area between the back of the parasphenoid and the aortic canal and underlie the ventral otic fissure. They are approximately rectangular in outline, with a more rounded anterior margin where they fit onto the ledge at the back of the parasphenoid. The left-hand plate has a narrow smooth ledge along its medial margin where it is overlapped by its partner. Both plates are covered in tubercular teeth, similar to those on the hind end of the parasphenoid. There is also a pair of accessory vomerine toothplates identical to those described in *Mimia*.

Parasphenoid: summary and discussion

The simplest form of actinopterygian parasphenoid is that seen in *Mimia* and *Cheirolepis* (Pearson & Westoll 1979), where it consists of a short, relatively broad toothed plate without a posterior stem or stalk and with no basipterygoid process (anterior ascending process), and in which the ascending process (posterior ascending process) does not extend across the oticosphenoid fissure onto the lateral commissure. It is further characterized by the presence of a spiracular groove on its buccal surface which terminates at or near the bucco-hypophysial canal.

A similar type of parasphenoid (without posterior stem or basipterygoid process, and where the ascending process does not reach the lateral commissure) is found in the rhipidistians *Eusthenopteron* (Jarvik 1954: fig. 18) and *Ectosteorhachis* (Romer 1937: fig. 4), the actinisitians *Nesides* (Stensiö 1963*b*: fig. 45), *Wimania* (Bjerring 1967: pl. 2B) and *Latimeria* (Millot & Anthony 1958), the dipnoans *Uranolophus* (Denison 1968: fig. 8) and *Dipnorhynchus* (Thomson & Campbell 1971: fig. 25), porolepids such as *Glyptolepis* and *Holoptychius* (Jarvik 1954: figs 19, 20), and the youngolepidids (Chang 1982). The structure called basipterygoid process in porolepids by Miles (1977: 159) is little more than the edge of the notch made by the

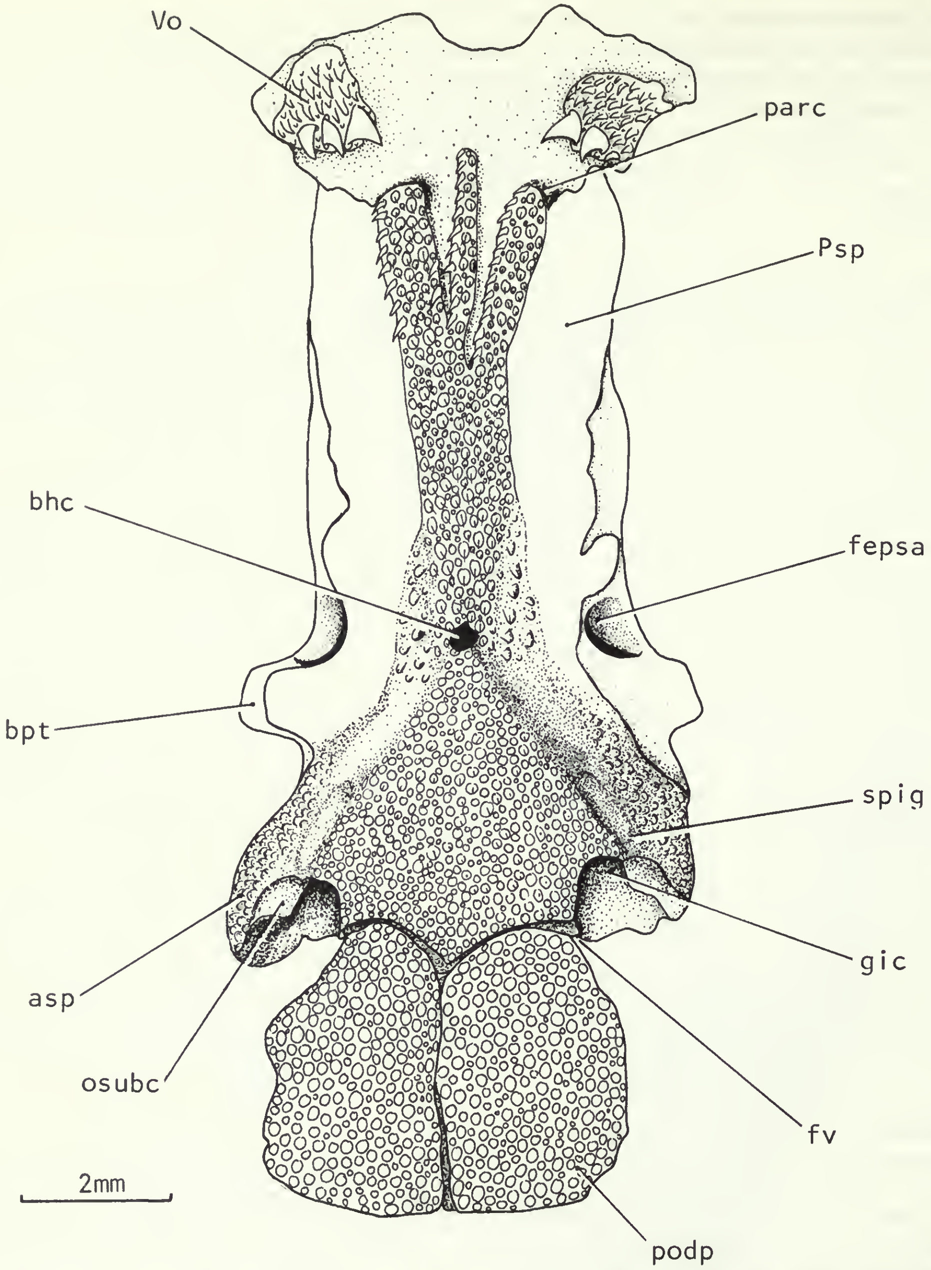


Fig. 51 *Moythomasia durgaringa* Gardiner & Bartram. Parasphenoid and associated structures in ventral view, from BMNH P.53221. After Gardiner & Bartram (1977).

passage of the efferent pseudobranchial artery. The spiracular groove (seen in *Moythomasia*, porolepids, *Youngolepis* and *Eusthenopteron*) is not present in actinistians or dipnoans, but its distribution in other osteichthyans and its presence on the neurocranium of *Acanthodes* (Miles 1973*a*) suggests it is a primitive osteichthyan feature. Thus the parasphenoid of *Moythomasia* and *Cheirolepis* must exemplify both the primitive actinopterygian and osteichthyan conditions.

The posterior elongation of the parasphenoid in post-Devonian actinopterygians has been

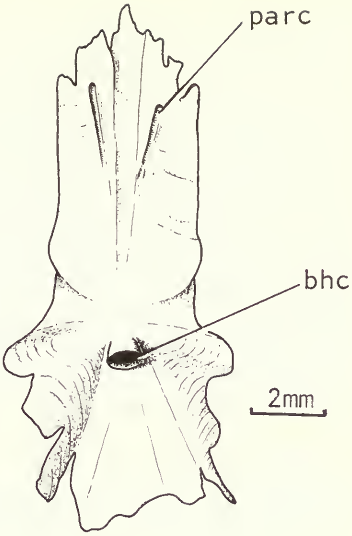


Fig. 52 *Moythomasia durgaringa* Gardiner & Bartram. Parasphenoid in dorsal view, from BMNH P.53217.

dealt with in detail by Gardiner (1973: 116), Patterson (1975: 527) and Miles (1977: 158), all of whom agree that elongation is the result of differential growth in phylogeny and that such a process occurred independently within the actinopterygians and dipnoans. In most post-Devonian palaeoniscids and in pholidopleurids this posterior extension never crossed the ventral otic fissure, but with the increase in size of the myodome the fissure came to lie further posteriorly (Gardiner & Bartram 1977: fig. 8) and consequently a short rounded stem developed behind the ascending process (*Pteronisculus*, Nielsen 1942; *Kentuckia*, Rayner 1951; *Boreosomus*, Nielsen 1942; *'Ambodipia'*, Beltan 1968; *Kansasiella*, Poplin 1974; *Coccolepis*, BMNH P.50822; *Australosomus*, Nielsen 1949). In other actinopterygians the stem of the parasphenoid is longer and extends across the fissure onto the ventral surface of the basioccipital (*Perleidus, Pachycormus,* parasemionotids, pholidophorids, Patterson 1975: 528). In *Polypterus*, living chondrosteans, *Paleopsephurus, Errolichthys* (Lehman 1952), *Chondrosteus* (RSM 1887.15.2), *Saurichthys* (Stensiö 1925), *Birgeria* (Nielsen 1949), pycnodonts, semionotids, caturids, *Amia, Lepisosteus* and most extant teleosts (Patterson 1975: 528) the parasphenoid floors the entire basioccipital and terminates beneath the occipital condyle. Similarly in *Bobasatrania* (Nielsen 1952) the parasphenoid extends back almost to the hind end of the neurocranium. The interrelationships of these actinopterygians possessing long-stemmed parasphenoids imply that the condition has been independently acquired on at least four occasions: in *Polypterus*, in *Birgeria*, in *Chondrosteus, Paleopsephurus* and living chondrosteans, and in neopterygians. A long stem has also been acquired on perhaps two other occasions: once in dipnoans (no stem in the Lower Devonian *Uranolophus*, Denison 1968) and possibly once within tetrapods (there is no stem in *Ichthyostega* according to Jarvik 1952; 1955: fig. 8).

1. *Parabasal canal.* Primitively in actinopterygians (and placoderms) neither the internal carotid nor the efferent pseudobranchial arteries pierced the parasphenoid. Instead the internal carotid artery entered the neurocranium behind the parasphenoid (in the short-stemmed forms) and passed forward between the parasphenoid and the basisphenoid in a short parabasal canal (*Cheirolepis, Mimia, Moythomasia, Pteronisculus, Australosomus*, etc.). The efferent pseudobranchial artery passed in above the parasphenoid and occasionally notched its lateral margin (*Mimia, Moythomasia*). In *Mimia* and *Moythomasia* the parabasal canal commences just behind the spiracular groove and a canal with precisely the same morphological relationships is also found in *Polypterus*, in the porolepid *Glyptolepis* (Jarvik 1972: fig. 19, cd.a.pal) and in *Youngolepis* (Chang 1982: fig. 7, c.a.ci). In *Glyptolepis*, however, the internal carotids passed

through the short stem of the parasphenoid into the parabasal canal through a foramen interpreted by Jarvik (1972: fig. 31) as having transmitted a medial branch of the internal carotid artery (see Gardiner 1973: 118). Anterior to the spiracular groove in *Glyptolepis* (prespiracular groove of Jarvik 1954, 1972; Bjerring 1971; but see Patterson 1975: 534; Gardiner & Bartram 1977: 243) and *Youngolepis* (Chang 1982: fig. 8B) the parasphenoid is notched by the passage of the efferent pseudobranchial artery (Gross 1936: 10A), though in some species of *Glyptolepis* (Jarvik 1972: fig. 31) this artery passed through the edge of the bone. A parabasal canal is also present in *Neoceratodus* (Holmgren & Stensiö 1936: fig. 288), *Griphognathus* (Miles 1977: fig. 50, c.i.?; fig. 56) and tetrapods (*Cryptobranchus*), and in dipnoans the efferent pseudobranchial artery enters the canal after passing in above the edge of the parasphenoid. A parabasal canal must therefore have been primitively present in osteichthyans and its subsequent loss in living chondrosteans, *Saurichthys, Latimeria* and *Eusthenopteron* (Jarvik 1954: fig. 6A, c.a.c.i) may be correlated with the narrowness of the parasphenoid in each of these fishes. A parabasal canal is not found in placoderms and is presumed to be a synapomorphy of osteichthyans.

2. *Internal carotid artery*. The backward growth of the parasphenoid in more advanced actinopterygians had a marked effect on the course of the internal carotids and associated arteries and at least four different topographies may be recognized (Gardiner 1973: 116).

In *Polypterus* the posterior stem of the parasphenoid is not only below the carotid arteries, but also below the dorsal arterial system and this condition is unique. In *Birgeria, Saurichthys, Saurorhynchus, Errolichthys, Chondrosteus* and *Paleopsephurus* a parabasal canal is missing and the stem of the parasphenoid as well as the ascending processes must have been above the carotid arteries as in *Acipenser*. In saurichthyids (Stensiö 1925; Gardiner 1960: fig. 21) and *Chondrosteus* (RSM 1887.15.2) there is a large, paired foramen in the parasphenoid beneath the posterior margin of the ascending process; this presumably transmitted the orbital artery (as originally suggested by Stensiö) and not the common carotid as Gardiner (1973: 116) and Patterson (1975: 331) have supposed. In *Lepisosteus* and *Amia* the efferent pseudobranchial and internal carotid arteries pass through notches in the lateral edges of the parasphenoid, into the parabasal canal (as in *Pteronisculus, Perleidus*, parasemionotids, caturids and *Lepidotes*) and the stem of the parasphenoid lies between the internal carotids. However, the internal carotid artery in *Boreosomus*, unlike all other described palaeoniscids, passed through a foramen in the base of the ascending process. This is a variation of the last condition. In *Dapedium*, pholidophorids, leptolepids and other primitive teleosts (Patterson 1975: 532) there are foramina in the parasphenoid for both the internal carotid and efferent pseudobranchial arteries and it appears that in these fishes the notches seen in more primitive forms such as *Perleidus*, parasemionotids, caturids and *Lepidotes* have become foramina, probably as a result of growth of the lateral edges of the parasphenoid. Conditions are similar in the porolepid *Glyptolepis* (Jarvik 1972: fig. 31). In advanced dipnoans the stem of the parasphenoid lies between the internal carotid artery and above the efferent pseudobranchial artery, much as in *Amia* and *Lepisosteus*. A similar relationship has been achieved in such tetrapods as *Cryptobranchus*, although here the carotid artery passes through a foramen in the lateral edge of the parasphenoid.

3. *Basipterygoid process*. An endoskeletal basipterygoid process is present in chondrichthyans, acanthodians and osteichthyans and is considered primitive for gnathostomes.

Primitively the osteichthyan skull possessed a well-developed endoskeletal basipterygoid process (*Mimia, Cheirolepis, Nesides, Glyptolepis, Eusthenopteron, Youngolepis*) but only in later, more advanced actinopterygians did it acquire support from the parasphenoid. Although the lateral angle of the parasphenoid in dipnoans may be in a similar topographic position to the actinopterygian dermal basipterygoid process, there is no reason to consider it homologous as Miles (1977: 159) has done. A dermal basipterygoid process is an actinopterygian specialization, possibly developed to reinforce the ventral wall of the myodome as originally suggested by Rayner (1951: 81). In the more primitive palaeoniscids and chondrosteans a dermal basipterygoid process is lacking (*Cheirolepis, Mimia, Moythomasia, Polypterus, Acipenser,* *Polyodon, Chondrosteus, Saurichthys, Errolichthys, Birgeria*), while in *Polypterus, Birgeria* and *Saurichthys* the endoskeletal basipterygoid process has also been reduced or lost.

A dermal basipterygoid process is first observed in some of the more advanced palaeoniscids and their relatives. Though small in *Boreosomus, Platysomus* and *Perleidus*, it is extensive in *Pteronisculus, Cosmoptychius* and *Kansasiella* (Poplin 1974: fig. 8) where the endoskeletal and dermal components are about equal. A similarly well developed dermal basipterygoid process, with a stout endoskeletal component above, is also present in *Dapedium* (Patterson 1975: fig. 112) and *Lepisosteus*, but in some caturids the process is very small (*Heterolepidotus, Caturus chirotes*, Rayner 1948: fig. 7) and in others it is absent (*Caturus furcatus, 'Aspidorhynchus', Macrepistius*). The basipterygoid process (dermal and endoskeletal) has also been lost in amioids, pachycormids and most Recent teleosts. By contrast in *Pholidophorus bechei* and *Lepidotes* (Patterson 1975: 529) the dermal basipterygoid process is very large and the endoskeletal part almost vestigial. In other pholidophorids and leptolepids the basipterygoid process is entirely dermal; a similar massive dermal process is found in a few other teleosts such as *Diplomystus*, osteoglossoids and ichthyodectids.

In summary, the endoskeletal basipterygoid process has been lost on several occasions; in *Polypterus*, in *Birgeria* and *Saurichthys*, in *Australosomus*, in caturids and amiids, in pachycormids and in later teleosts. The dermal basipterygoid process must also have been lost on more than one occasion (amiids, pachycormids and several teleosts groups).

4. *Ascending process*. This is another important outgrowth of the parasphenoid in actinopterygians, developed primarily in relation to the spiracular diverticulum and which reinforces the outer wall of the myodome. Such an ascending process (or posterior ascending process) is a specialized feature developed within the group. Primitively in osteichthyans it was very short and did not extend across the ventral otic fissure in *Mimia* and *Cheirolepis*, porolepids (*Glyptolepis*, Gross 1936: pl. 8), youngolepidids (Chang 1982: fig. 7), osteolepids (*Eusthenopteron*, Jarvik 1954: fig. 18) and Devonian actinistians (*Diplocercides*, Bjerring 1972: fig. 3A). Only in later actinopterygians and *Polypterus* is a long ascending process developed.

There has been considerable confusion over the identification of the ascending process. Stensiö (1925: 85) called the ascending process on the parasphenoid of sturgeons and *Saurichthys* the 'processus ascendens posterior', but homologized the same process in *Amia* and *Lepisosteus* with the dermal basipterygoid process of palaeoniscids and so called it the 'processus ascendens anterior'. The view that the ascending process in *Amia* is not comparable to that in *Acipenser* received support from Pehrson (1940: 38) and Holmgren (1943: 39), but Nielsen (1942: 106; 1949: 84) and Rayner (1951: 81) demonstrated that the two are strictly homologous. Jarvik (1954: 51) considered the ascending process of the rhipidistian and actinistian parasphenoid to be the homologue of the basipterygoid process of the parasphenoid in *Pteronisculus*, referring to it as the anterior ascending process. But as Patterson (1975: 533) and Gardiner & Bartram (1977: 243) have shown, it is homologous with the ascending process of primitive actinopterygians.

A true ascending process (one which crosses the oticosphenoid fissure) is first met with in *Moythomasia* and *Kentuckia*, where the slender process extends onto the lateral commissure but terminates level with the bottom of the jugular canal. In more advanced palaeoniscids such as *Kansasiella, Pteronisculus, Boreosomus* and in *Australosomus* the ascending process is more extensive and its tip approaches or enters the lower opening of the spiracular canal. In *Polypterus*, where the spiracle is unconstricted, the ascending process is large and very complicated (Jarvik 1954) and may be assumed to have had a different history from that of *Birgeria, Saurichthys* and living chondrosteans, where it covers a major part of the otic and orbitotemporal walls.

In more advanced actinopterans such as *Perleidus*, parasemionotids, semionotids and caturids (Patterson 1975: 533) the ascending process, though as extensive as in most palaeoniscids, is less stout and often more distinctly grooved by the spiracular diverticulum. The ascending process in pholidophorids, leptolepids (Patterson 1975: 519), pachycormids (Patterson 1975: fig. 106) and *Ichthyokentema* (Patterson 1975: fig. 150) on the other hand is shorter and terminates below the spiracular canal when the latter is present. The ascending process in most Recent teleosts is also short, but occasionally it is enlarged and meets the frontal as in *Gasterosteus* and *Arapaima*. Patterson (1975: 534) has suggested that the ascending process may be reduced in height in teleosts as a result of the reduction in the spiracular diverticulum. Whether or not this is true, there is little doubt that the ascending process has developed on at least two occasions within actinopterygians, once in *Polypterus* and once in the actinopterans.

The spiracular grooves on the ascending processes of *Moythomasia* are continued onto the ventral surface of the parasphenoid (Fig. 51), where they join around the lower opening of the bucco-hypophysial canal on a level with the efferent pseudobranchial foramina. The spiracular grooves are linked by a transverse groove in *Pholidophorus bechei* and the Sinemurian *Leptolepis* (Patterson 1975: figs 62, 143). A corresponding groove is found in the porolepids *Holoptychius* (Gross 1936: fig. 10A), *Glyptolepis* (Jarvik 1972: fig. 31) and *Porolepis* (Jarvik 1972: pl. 9), and in *Youngolepis* (Chang 1982: fig. 8). Teeth occur in the spiracular groove of *Moythomasia* (Fig. 51), some specimens of *Pteronisculus, Perleidus* (Patterson 1975: fig. 115) and on the ventral plate of the ascending process in the mouth of the spiracular cleft in *Polypterus*. Teeth are also present in the transverse groove in *Moythomasia, Glyptolepis* and *Youngolepis*. Some confusion has resulted from the misidentification of this transverse groove in rhipidistians, where it has been designated 'prespiracular' by Jarvik (1954, 1972) and Bjerring (1971, 1977), but as Patterson (1975: 534) and Gardiner & Bartram (1977: 243) have demonstrated, the groove is homologous with that in actinopterygians and is therefore a spiracular groove. Although it is absent in dipnoans and actinistians, the occurrence of this groove in actinopterygians, porolepiforms and youngolepidids suggests that it is a primitive osteichthyan character.

A similar transverse groove is present on the parasphenoid of placoderms (Kulkzycki 1956: pl. 1G; Miles & Westoll 1968: fig. 18a; White & Toombs 1972: figs 5, 6, 7; Young 1979: pl. 5). This has been variously interpreted as having housed blood vessels (Kulkzycki 1956: 107; Stensiö 1963*a*: 122) or outgrowths of the hypophysial stalk (White & Toombs 1972: 388). Nevertheless, it bears the same relationship to the bucco-hypophysial canal as in many osteichthyans and the presence of teeth along its borders (White & Toombs 1972: fig. 5) suggests it is a spiracular groove.

5. *Parasphenoid teeth*. The entire oral surface of the parasphenoid is toothed in *Mimia* (Fig. 50) and *Cheirolepis*. In *Moythomasia*, however, although the posterior region is completely toothed, anterior to the lower opening of the bucco-hypophysial canal the teeth are confined to a narrow, central band (Fig. 51). In *Polypterus* teeth occupy the full width of the parasphenoid anteriorly, but beneath the orbit they are restricted to a narrow band similar in extent to that in *Moythomasia*. Posteriorly this band separates into two curved bands of teeth which run along the anterior edges of the ventral plate of the ascending process (Allis 1922: fig. 9). In most other palaeoniscids, parasemionotids and the majority of caturids the parasphenoid is toothed from the level of the ascending process forwards. Reduction and loss of parasphenoid teeth has occurred on several occasions within the actinopterygians. Thus the teeth are reduced to a small tooth patch around the lower opening of the bucco-hypophysial canal in *Saurichthys* and are completely wanting in *Birgeria, Chondrosteus* and living chondrosteans. Parasphenoid teeth are also missing in *Australosomus, Bobasatrania*, pycnodonts, *Macrepistius, Ichthyokentema, Catervariolus* and most teleosts (Patterson 1975: 529).

In Devonian and Carboniferous actinistians and in *Eusthenopteron* the parasphenoid has a tooth-bearing median ridge which extends back to enclose the lower opening of the bucco-hypophysial canal. In later actinistians and in some osteolepids (*Ectosteorhachis, Megalichthys*) the tooth-bearing ridge is confined to the area in front of the bucco-hypophysial canal. In *Youngolepis* (Chang 1982: fig. 8) the parasphenoid is completely toothed but in porolepids such as *Glyptolepis* (Jarvik 1972: fig. 31) the tooth patch is restricted to the area around the opening of the bucco-hypophysial canal and, as in *Elops*, there are in addition numerous small toothplates in the roof of the oral cavity. In *Porolepis* (Jarvik 1972: fig. 65), however, the teeth are reduced to a median row of some eight large teeth borne on a raised area; parallel enlargement and specialization of parasphenoid teeth is seen in various teleosts (e.g. albulids, hiodontids, osteoglossids).

In the Lower Devonian dipnoan *Uranolophus* (Denison 1968: fig. 8) the buccal surface of the parasphenoid is toothed except posteriorly where there is a small area of smooth bone, whereas in the other Lower Devonian form (*Dipnorhynchus*) the buccal surface has a continuous dentine covering (Campbell & Barwick 1982). In many dipnoans with a stalked parasphenoid the buccal surface is covered with teeth whereas the posterior stem is smooth (*Griphognathus, Holodipterus* Miles 1977: 151, 154). In *Dipterus valenciennesi* (White 1965) the bucco-hypophysial duct opens in the anterior portion of this toothed area. In *Conchopoma* the toothed anterior portion is expanded and opposed to the median basibranchial toothplate (Denison 1969: 199), but in *Chirodipterus* (Miles 1977: 153) the parasphenoid teeth have been entirely lost.

In placoderms the parasphenoid may be completely covered by numerous small teeth as in *Buchanosteus* (White & Toombs 1972: fig. 5; Young 1979: pl. 5) and *Kujdanowiaspis* (Jarvik 1954: fig. 34).

Primitively, therefore, in osteichthyans and placoderms the oral surface of the parasphenoid was toothed.

6. *Bucco-hypophysial canal.* The bucco-hypophysial duct opens through the parasphenoid into the roof of the mouth in primitive actinopterygians (*Mimia, Moythomasia, Cheirolepis, Polypterus, Saurichthys, Chondrosteus, Perleidus*), and this opening is retained in more advanced forms such as '*Aspidorhynchus*', *Dapedium, Lepidotes, Caturus, Heterolepidotus* and *Elops* (Patterson 1975: 530).

An open bucco-hypophysial duct is also characteristic of most actinistians (*Nesides, Latimeria*), all described porolepids (Jarvik 1972), and *Youngolepis* (Chang 1982), *Eusthenopteron* (Jarvik 1954), *Dipterus* and *Ichthyostega* (Säve-Söderbergh 1932). In *Glyptolepis* (Jarvik 1972: fig. 19D) the opening is paired.

The parasphenoid also contains an open bucco-hypophysial canal is placoderms. White & Toombs (1972: fig. 6) figured a paired opening for the bucco-hypophysial canal in *Buchanosteus*, but Young (1979: fig. 17; pl. 5) has shown, in better preserved material, that the opening, although bilobed, is single.

The striking similarity between the placoderm and osteichthyan parasphenoids (teeth, spiracular grooves, and foramen for bucco-hypophysial canal) suggests that a parasphenoid is a synapomorphy of a group containing osteichthyans and placoderms.

7. *Subcephalic muscles.* Nelson (1970*a*: 468) has suggested that the subcephalic muscles of *Latimeria*, which extend beneath the intracranial joint from the otico-occipital to the parasphenoid, may be derived from one or more of the anterior body myomeres such as occur in *Polypterus*. In *Polypterus* the body musculature extends forwards beneath the occipital and otic regions, to be inserted on the parasphenoid immediately behind the ascending process. It thus spans the ventral otic fissure which lies above the parasphenoid. The area of muscle insertion lies between the posterior margin of the ascending process and the stem of the parasphenoid.

A distinct notch is present in the posterior margin of the parasphenoid in *Mimia* and *Moythomasia*, in the latter immediately behind the ascending process, and below and anterior to the articulation for the first infrapharyngobranchial; it may be inferred that subcephalic muscles of the type found in *Polypterus* were inserted in this region (osubc, Figs 50, 51). This notch may also be identified by the same topographic and morphological criteria as have been used to recognize the insertion of the subcephalic muscles in rhipidistians and actinistians (Bjerring 1967, 1971; Jarvik 1966, 1972).

Bjerring (1971: fig. 6), however, taking *Latimeria* as his model, has restored subcephalic muscles in *Pteronisculus* inserting on the hind end of the parasphenoid, but originating on the underside of the basioccipital in the triangular area circumscribed by the grooves for the lateral dorsal aortae (and thereby spanning the ventral otic fissure as in *Latimeria*). Patterson (1975: 538) suggested that although such an area on the basioccipital could well have served for muscle attachment it does not follow that the muscles were directed forwards and proposed that it was more likely that it served for the attachment of anterior trunk muscles, serially homologous with those attaching to the back of the parasphenoid in *Polypterus*. In my opinion this triangular area of the basioccipital (primitive for actinopterygians; Patterson 1973: 558) never served for muscle attachment in actinopterygians. It lies above the general level of the floor of the occipital region in *Mimia* (Fig. 13), *Moythomasia* (Fig. 7) and *Kentuckia* (Rayner 1951: fig. 9); it never shows any sign of muscle scars, is frequently fenestrated (Figs 14, 15, 50) and in *Moythomasia* (Fig. 51) the paired parotic toothplates neatly fill in the area between the back of the parasphenoid and the aortic canal. Furthermore this triangular area, although domed in *Mimia* and *Moythomasia*, is depressed and smooth in *Pteronisculus* (Nielsen 1942: fig. 6) and *Kentuckia* (Rayner 1951: fig. 9). Thus it appears that a subcephalic muscle of rhipidistian type originating on the underside of the occipital ossification did not exist in actinopterygians, and I suggest that the foremost trunk myomere inserted on the posterior part of the parasphenoid only, as in *Polypterus*, and not on the underside of the occipital ossification.

Distinct pits in a similar position to the notches in *Mimia* and *Moythomasia* occur on the underside of the parasphenoid of *Cosmoptychius* (Schaeffer 1971: fig. 8A) and *Coccolepis* (BMNH P.50822), immediately behind the bucco-hypophysial canal and medial to the internal carotid foramen. There is a pair of pits in this position in several more advanced actinopterans including *Heterolepidotus, Caturus chirotes* (Gardiner 1960: fig. 36, eff.pseud.), *Lepidotes latifrons, Pholidophorus bechei* and *Ichthyokentema* (Patterson 1975: 535; figs 62, 150). In other pholidophorids, leptolepids and pachycormids the pits are more posteriorly placed. Thus I conclude that subcephalic muscles of the type found in *Polypterus* were primitively present in actinopterygians and inserted on the posterior part of the parasphenoid. Identically-placed pits to those seen in *Cosmoptychius* and *Pholidophorus* occur in the osteolepids *Megalichthys, Ectosteorhachis* (Romer 1937: fig. 4, ci), *Eusthenodon* (Bjerring 1967: pl. 2C) and *Eusthenopteron* (Bjerring 1967: pl. 2A), but there is no reason to assume that the muscles inserting in these pits were more like those of *Latimeria* than of *Polypterus*, particularly since the area of muscle insertion in *Latimeria* is far in advance of the bucco-hypophysial canal.

In other actinopterygians such as *Perleidus* and parasemionotids there is a much wider, irregular recess (Patterson 1975: 536; figs 98, 116) for the subcephalic muscles; this condition is paralleled by the porolepids *Glyptolepis* and *Porolepis* (Jarvik 1972: 86) and by *Youngolepis* (Chang 1982: figs 7, 8), where there is a similar recess behind the spiracular groove, implying a broad insertion. This has prompted Patterson (1975: 538) to postulate that a broad insertion may be the primitive condition.

8. *Accessory toothplates*. In *Mimia* (Av, Fig. 53), *Moythomasia, Elonichthys* (Watson 1925: fig. 22, D.Pt$_1$), *Pteronisculus* (Nielsen 1942: fig. 34) and *Australosomus* (Nielsen 1949: fig. 26) there is a large toothplate between the entopterygoid and parasphenoid (see p. 271), which I have termed the 'accessory vomerine toothplate'. The occurrence of such a toothplate is considered primitive for actinopterygians.

In chondrichthyans there is a shagreen of small denticles in the skin of the roof of the mouth (Nelson 1970*b*: 2) and in the porolepid *Glyptolepis* (Jarvik 1972: figs 8C, D, 16, 22, 30) there are numerous small dental plates. Similarly in *Elops* (Nybelin 1968) there is a small patch of toothplates lying free in the mucous membrane in the region of the bucco-hypophysial canal. Thus primitively in gnathostomes there must have been numerous small dental plates in the skin lining the roof of the mouth. In early actinopterygians some of these are presumed to have been replaced by a single accessory vomerine toothplate.

Paired toothplates also occur in the roof of the mouth immediately behind the short parasphenoid of primitive osteichthyans. These paired parotic plates are found in *Moythomasia* (Fig. 51) and *Eusthenopteron* (Jarvik 1954: fig. 22).

Palatoquadrate and dermal bones of the cheek

Mimia toombsi

In *Mimia* the palatoquadrate is very long; anteriorly it articulates with the lateral ethmoid (apal, Fig. 50) while its posterior part reaches beyond the occiput (Fig. 55). In the majority of specimens the palatoquadrate is ossified throughout as one bone, as in the larger specimens of

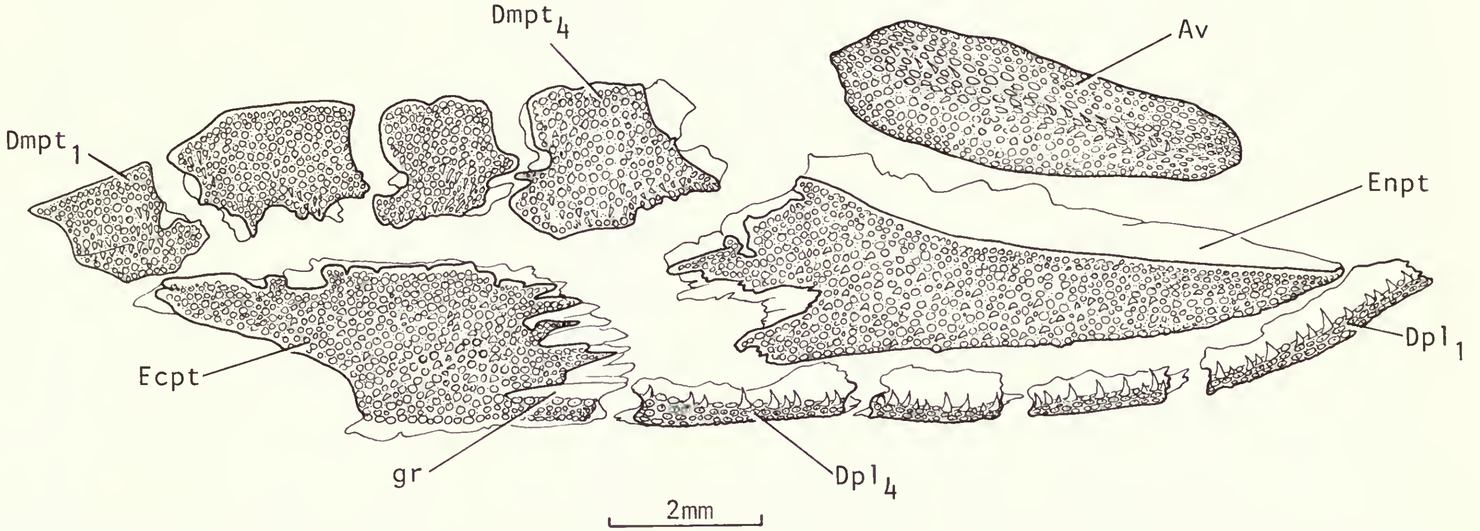

Dmpt$_4$
Av
Dmpt$_1$
Enpt
Dpl$_1$
Ecpt
gr
Dpl$_4$
2mm

Fig. 53 *Mimia toombsi* Gardiner & Bartram. Dermal bones of the left palate of an incompletely ossified individual in medial view, from BMNH P.56473.

Pteronisculus and *Australosomus* (Nielsen 1942: 143; 1949: 99) and as in specimens of *Eusthenopteron* and *Glyptolepis* (Jarvik 1954: 27; 1972: 70). In all these specimens it is impossible to detect ossification centres. Two smaller specimens of *Mimia*, however, show three separate ossifications: one in the quadrate region (Fig. 57), one in the metapterygoid region and one in the autopalatine region; these three ossifications were separated in life by a large area of cartilage. In one or two other specimens the junctions between these bones may be inferred.

The quadrate appears to have been the most prominent ossification in the palatoquadrate cartilage, with its centre of ossification in the condyle region. The quadrate forms the inner margin of the adductor mandibulae fossa, and reaches anterodorsally to the level of the hole for the basipterygoid process. Here it meets the much smaller autopalatine ossification, the junction being marked by a prominent ridge. The centre of ossification of the metapterygoid lies dorsally around the fossa for the levator arcus palatini muscle and ventrally this bone extends to just below the spiracular groove (spig, Fig. 56). Anteriorly the metapterygoid forms the posterior margin of the hole for the basipterygoid process, the anterior margin being formed by the autopalatine. Thus the quadrate is the largest endoskeletal ossification, the metapterygoid is somewhat smaller and the autopalatine considerably less extensive. In this respect *Mimia* resembles *Acanthodes* (Miles 1965: fig. 1).

The palatoquadrate ossification is roughly triangular in its outline with a circular hole (hbpt, Fig. 56) in the anterodorsal margin. During life the basipterygoid process slid through this hole which functioned as a guide during lateral movements of the palatoquadrate. A similar hole has been described in the palate of certain species of *Pteronisculus* and *Boreosomus* by Lehman (1952: figs 35, 57) and in the palate of *Kentuckia* by Rayner (1951: fig. 3), but unlike *Pteronisculus* (Nielsen 1942: fig. 35) and *Kentuckia* there is no additional process on the palate in this region.

The posterior division of the palatoquadrate forms a high, nearly vertical plate which is curved dorsally so that its anterolateral face is concave in a dorsoventral and a rostrocaudal direction and its medial face is correspondingly convex. The concavity in the anterior face of the

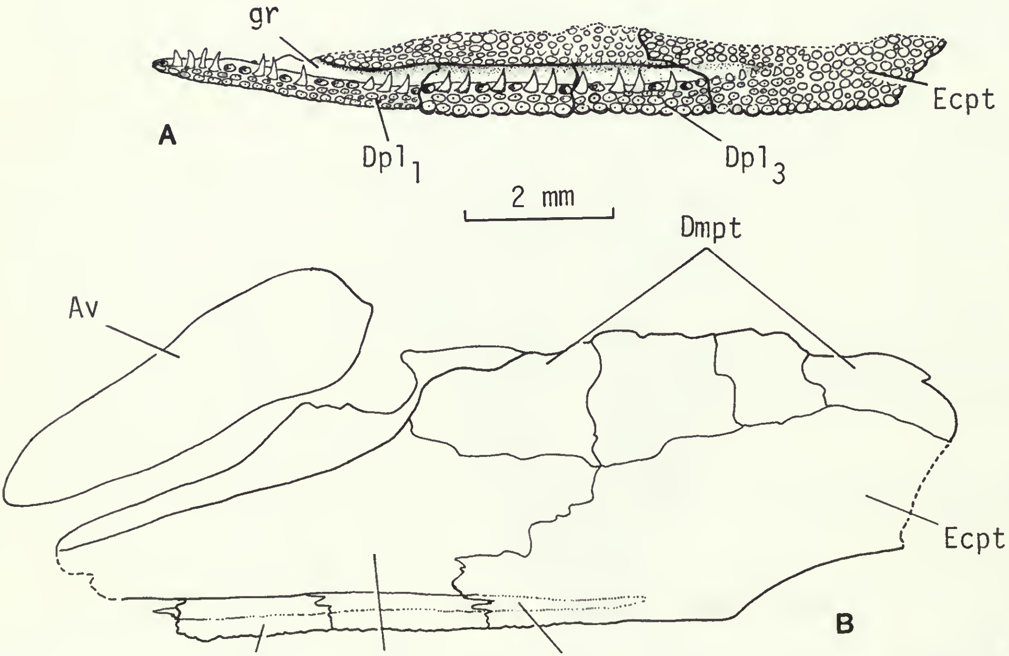


Fig. 54 *Mimia toombsi* Gardiner & Bartram. Dermal bones of the right palate in medial view. (A), from BMNH P.56490; (B), from BMNH P.56486.

metapterygoid (lapf, Fig. 56) presumably served for the insertion of the levator arcus palatini muscle. A similar concavity is recognizable in *Pteronisculus* and *Australosomus* (Nielsen 1942: 144; 1949: 102). The whole of the posterior margin of the palatoquadrate is in contact with the medial face of the preopercular and ventrally with the medial face of the quadratojugal (Fig. 57). This junction is often so complete that the preopercular and quadratojugal are immovably fixed to the palatoquadrate (Fig. 60). Ventrally the palatoquadrate forms the medial boundary of the opening for the adductor mandibulae, but anterior to this fossa it is in contact with the medial face of the ventral part of the maxilla. As with the preopercular, the junction is often so complete that the maxilla is fused to the palatoquadrate. This junction is further strengthened by fusion of the dermopalatines with both the overlying palatoquadrate and the maxilla (Figs 56, 60).

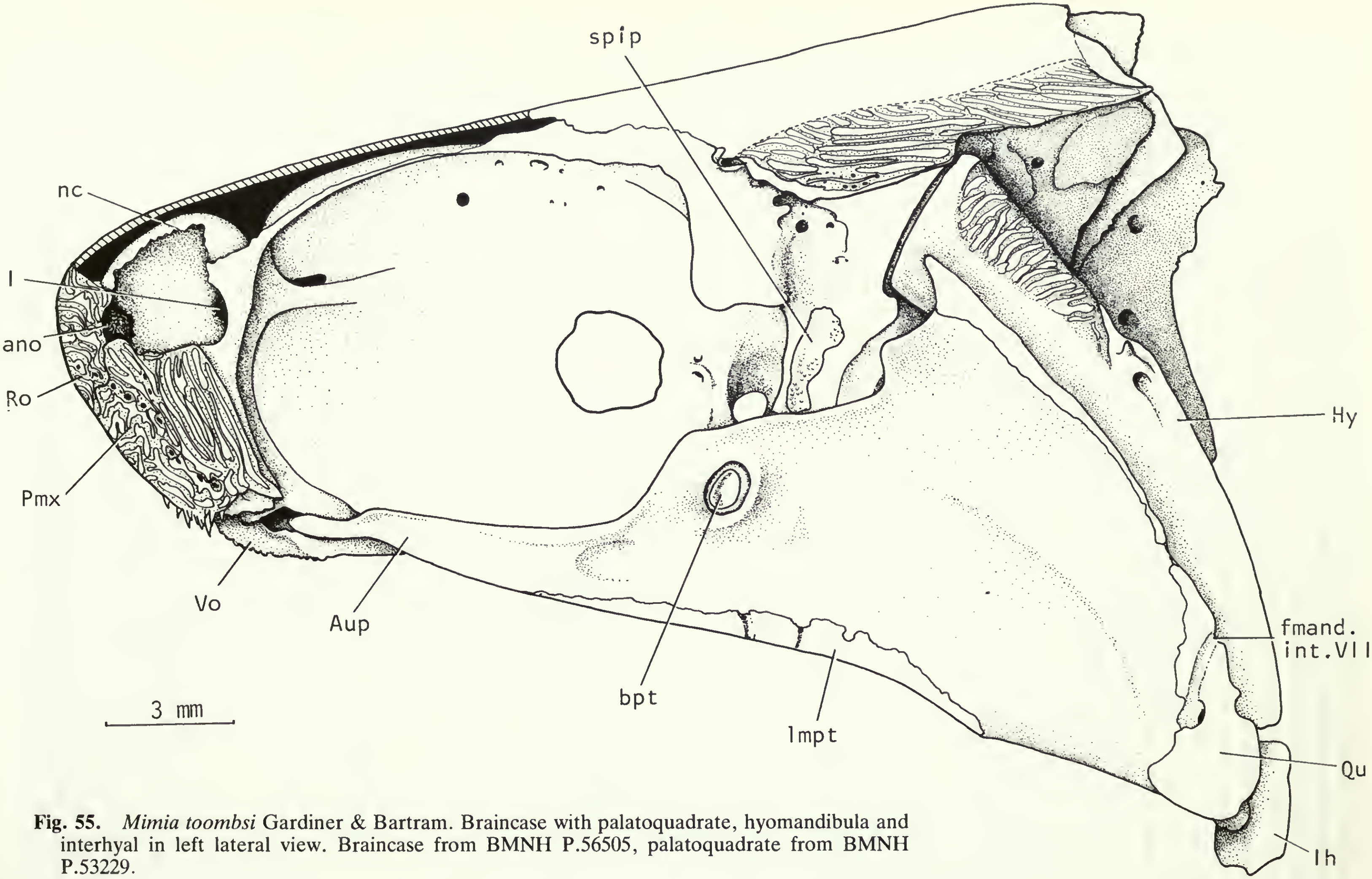
In the metapterygoid region there is a gradual transition between the dorsal, laterally bent part and the vertical or quadrate part of the palatoquadrate ossification, but there is no distinct angle between these two regions as there is in *Pteronisculus* (Nielsen 1942: 145). On the medial side of the metapterygoid region there is a conspicuous groove running back from the hole for the basipterygoid process down onto the quadrate (spig, Figs 56, 57). A similar groove has been figured in *Pteronisculus* (Nielsen 1942: figs 35, 36). Gardiner (1973: fig. 8, icg) originally attributed this groove to the internal carotid artery, but from its position just dorsal to the tooth-bearing sheet of dermal bone it is more probable that it represents the lateral surface of the ventral end of the spiracular diverticulum. A similar groove on the parasphenoid (spig, Fig. 50) is apparently a continuation of the groove on the metapterygoid. In *Porolepis* and *Eusthenopteron* (Jarvik 1954: fig. 16, resh) there is a similar groove on the palate which has been called the spiraculo-hyomandibular recess by Jarvik, and as in *Mimia* and *Pteronisculus* this groove is in the same position as the posterior division of the spiracular slit in *Polypterus*.

The posterodorsally-facing margin of the palatoquadrate ossification is pierced by several short transverse canals. In the metapterygoid and in the dorsal region of the quadrate there are two such canals (fmand.int. VII, Figs 55, 56, 57), while ventrally in the quadrate there is either a single canal or a pair of canals immediately above the condyles (fmand.int. VII, Fig. 57). These canals presumably transmitted the internal mandibular branch of the facial nerve as in *Polypterus* (Allis 1922: 282), the dorsal pair of foramina serving for the entrance of that nerve and the ventral pair for its exit. A single short transverse canal and groove has also been described in *Pygopterus* (Aldinger 1937: 145) and *Pteronisculus* (Nielsen 1942: 145). Lateral to the posterior end of the spiracular groove and immediately above these transverse canals lay the hyomandibula with the interhyal beneath it (Hy, Ih, Fig. 55); ventrally the quadrate articulated with the lower jaw by a double-headed joint, the facets or condyles of which lie lateral to one another as in *Pteronisculus* (Nielsen 1942: fig. 33) and *Eusthenopteron* (Jarvik 1954: fig. 25).

That part of the palatoquadrate ossification in front of the point of junction with the basipterygoid process is mostly formed by the autopalatine. This forms a thin plate of bone, concave dorsolaterally and convex ventromedially. Posteriorly the limit of the autopalatine is marked by a distinct ridge behind which there is a somewhat deeper concavity in the lateral surface. This concavity immediately in front of the hole for the basipterygoid process marks the most anterior insertion point of the adductor mandibulae muscle. Anteriorly the autopalatine turns inwards to articulate with the lateral ethmoid by a cartilaginous interface.

Like the cartilage bones, in most specimens the dermal toothplates on the medial surface of the palatoquadrate are ossified throughout as one bone, and closely resemble those of *Eusthenopteron* (Jarvik 1954: fig. 16), except that in the latter there are separate dermopalatines. In two specimens, however, individual bones are apparent: in one there are nine and in the other ten (Fig. 53), four dermometapterygoids, an entopterygoid, an ectopterygoid and three or four dermopalatines.

The entopterygoid (Enpt, Figs 53, 54) is the largest of the dermal bones on the oral face of the palatoquadrate. It is approximately triangular in outline and tapers to a point anteriorly where it rests against the anterior end of the autopalatine. Like the pterygoid of *Eusthenopteron* and *Glyptolepis* (Jarvik 1972: fig. 25), in the adult it fuses indistinguishably with the underlying autopalatine and metapterygoid. However, neither the entopterygoid nor the underlying dermopalatine reach the anterior limit of the autopalatine. The entopterygoid is broadest


spip
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bpt
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Fig. 55. *Mimia toombsi* Gardiner & Bartram. Braincase with palatoquadrate, hyomandibula and interhyal in left lateral view. Braincase from BMNH P.56505, palatoquadrate from BMNH P.53229.

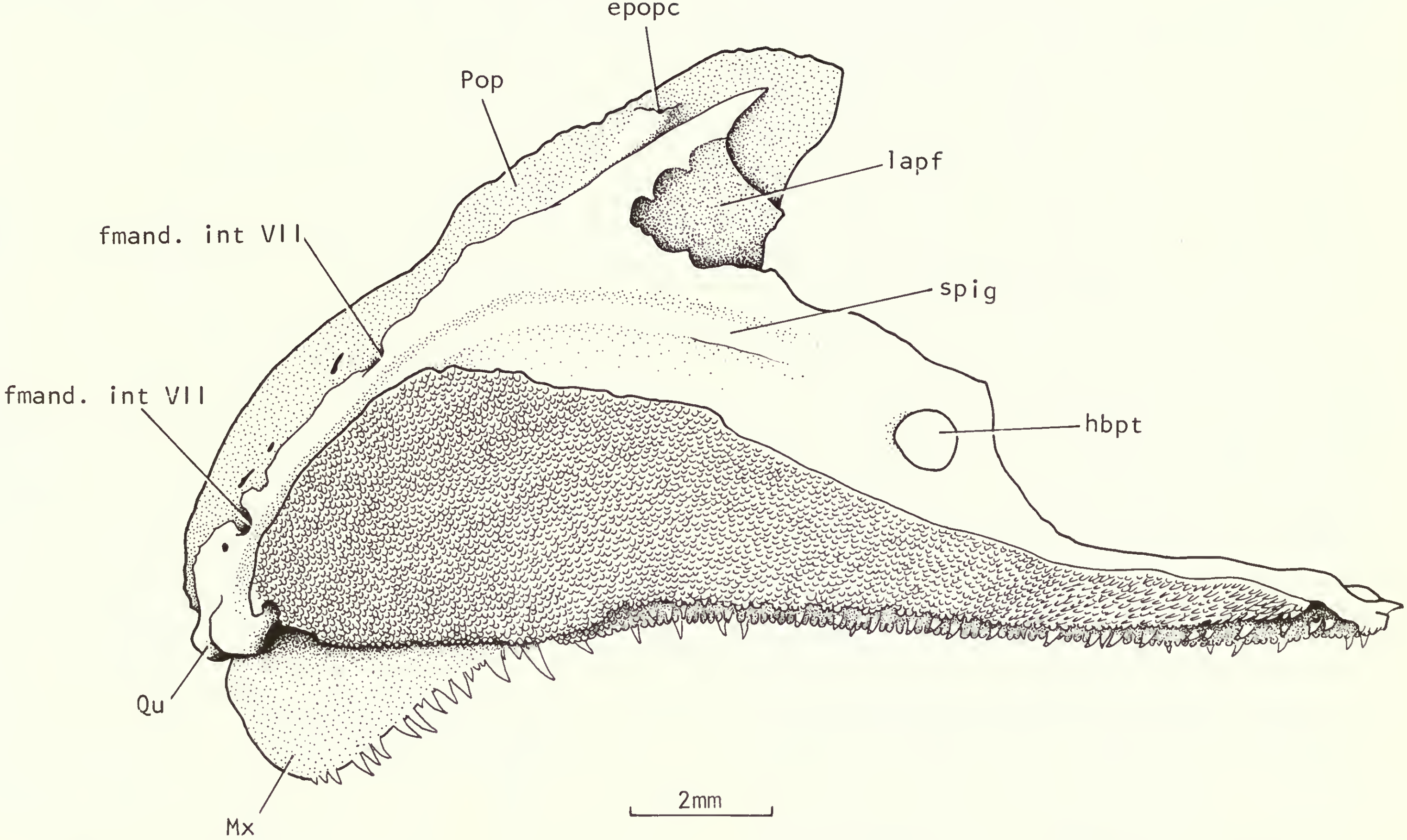
epopc
Pop
lapf
fmand. int VII
spig
fmand. int VII
hbpt
Qu
Mx
2mm

Fig. 56 *Mimia toombsi* Gardiner & Bartram. Left palatoquadrate and associated dermal bones in medial view, from BMNH P.56498.

posteriorly where it interdigitates with the ectopterygoid and the anteriormost dermometapterygoid. Medially it is covered by closely-set, small teeth, similar to those on the parasphenoid, except for a shelf-like margin of thin bone dorsally. Posteriorly this untoothed margin terminates in a small process (Fig. 53) which fits beneath the anterior margin of the hole for the basipterygoid process. A similar anterior process on the anteriormost dermometapterygoid forms the hind margin of this hole. The accessory vomerine toothplate (Av, Figs 53, 54) fits loosely on this dorsal margin of the entopterygoid, spanning the gap between it and the parasphenoid. The radiation centre of the entopterygoid lies near the dorsomedial margin, but more posteriorly than in *Pteronisculus* (Nielsen 1942: fig. 37). Ventrally the entopterygoid adjoins the dermopalatines and covers a marginal zone of the oral face of these bones, but leaves a well-marked groove (gr, Figs 53, 54) between it and the dermopalatine tooth row.

There are four dermometapterygoids (Dmpt, Figs 53, 54) which rest against the medial face of the metapterygoid and quadrate, and in adult fish fuse indistinguishably with them and one another and with the ectopterygoid. The two anterior dermometapterygoids lie well below the spiracular groove, but the two posterior bones form the lateral edge of the spiracular gill slit. All four bones interdigitate with one another; the anteriormost also interdigitates with the entopterygoid while the three more posterior elements suture with the ectopterygoid ventrally. All three posterior bones are completely covered by small, closely set teeth.

The ectopterygoid (Ecpt, Figs 53, 54) covers the posteroventral part of the oral face of the palatoquadrate. Caudally the bone extends almost as far as the posterior dermometapterygoid, but rostrally it terminates before the basipterygoid articulation and the anteriormost dermometapterygoid. Posteriorly the ectopterygoid lies against the vertical oral face of that part of the quadrate which bounds the adductor fossa. Immediately in front of the adductor opening the ventral part of the ectopterygoid is turned under and outwards to form an almost horizontal external lamina. This lamina sutures with the maxilla, overlapping a narrow marginal zone of the

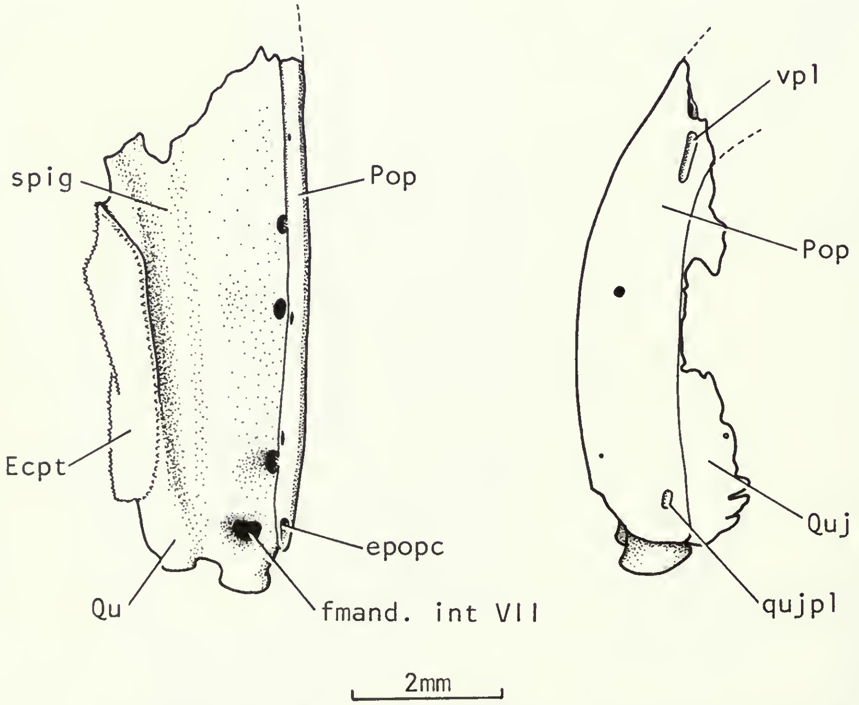

Fig. 57 *Mimia toombsi* Gardiner & Bartram. Quadrate region of palatoquadrate and associated dermal bones in posterior (left) and lateral views, from BMNH P.53254.

internal horizontal lamina. Anteriorly the ectopterygoid sutures with the posterior dermopalatine and the entopterygoid. The dorsal margin is sutured to the three posterior dermometapterygoids while the anterodorsal corner of the ectopterygoid just reaches the anteriormost dermometapterygoid. The entire oral face of the bone is covered by closely set, pointed teeth, apart from a narrow groove anteriorly (gr, Fig. 53). This groove is continuous with a similar groove in the dorsal margin of the dermopalatines (Fig. 54). The centre of ossification lies at the posteroventral corner, in front of the adductor opening where the ectopterygoid contacts the maxilla.

The dermopalatines form a series of three or four interdigitating bones which provide an anterior continuation of the horizontal external lamina of the ectopterygoid. The lateral margins of the dermopalatines overlap a narrow marginal zone of the internal horizontal lamina of the maxilla and their medial margins are overlapped orally by the entopterygoid. Laterally the dermopalatines are covered by small, closely set pointed teeth, medial to which is a series of much larger pointed teeth. The internal lamina beyond the tooth row is devoid of teeth and forms a well-marked groove (gr, Fig. 54) between the toothed area and the overlapping entopterygoid. The centre of ossification of each dermopalatine lies more or less at the middle of the bone.

The maxilla is of the usual palaeoniscid type (also seen in onychodonts, Jessen 1966) in which there is a narrow suborbital part and a high posterior expansion (Fig. 60). The suborbital portion is longer than in *Cheirolepis, Moythomasia* and *Pteronisculus*. The dorsal and posterior margins of the posterior expansion overlap a considerable portion of the lower margin of the quadratojugal (Fig. 63) so that only a small part of the quadratojugal is visible. The suborbital extension of the maxilla is overlapped by the posteroventral margin of the jugal and by the lachrymal. A horizontal longitudinal lamina stretches along the medial, ventral margin of the maxilla from the anterior margin of the adductor fossa to the anterior limit of the bone. The lamina increases in breadth as it passes anteriorly but narrows again from the level of the basipterygoid process anteriorly. The maxilla is connected by its horizontal lamina with the ectopterygoid and dermopalatines, as in *Pteronisculus* (Nielsen 1942: fig. 35). The ventral edge of the palatoquadrate sits above this horizontal, longitudinal lamina and in the quadrate region is produced dorsally into a flattened flange (lmpt, Fig. 55) which is attached to the inner surface of the maxilla. This quadrate flange stretches from the adductor fossa to the posterior limit of the autopalatine and is intimately connected with the maxilla. Ventrally the free margin of the maxilla bears teeth; the largest teeth occur at the anterior end of the posterior expansion and the smallest posteriorly. An outer series of much smaller teeth grades almost imperceptibly into the surface ornamentation. The radiation centre of the maxilla lies above the horizontal lamina and just anterior to the expanded posterior region (see Fig. 66, *Moythomasia*).

The preopercular is a long, acutely angled bone which extends forwards above the posterior expansion of the maxilla and carries the preopercular canal which is directed towards the otic portion of the infraorbital canal (temporal canal). Its anteroventral margin overlaps the quadratojugal (Figs 60, 61, 63) to such an extent that this latter bone is difficult to recognize in lateral view. The preopercular canal does not run the whole length of the bone as it does in *Pteronisculus* (Nielsen 1942: fig. 27), but instead exits dorsally before reaching the anterodorsal margin (epopc, Figs 56, 63). The canal runs parallel to the posterodorsal margin, piercing the radiation centre. From close to the radiation centre the horizontal pit-line passes anteriorly towards the anterior margin of the preopercular. Internally, it is marked by a small but distinct branch of the preopercular canal (bpopc, Fig. 63). In some specimens a short vertical pit-line (vpl, Fig. 61) joins the horizontal pit-line posteriorly, but in others the two lines are separate (Fig. 62). The preopercular is thickened internally along the route of the preopercular canal and it is this region which is in intimate contact with the palatoquadrate. Both the metapterygoid and quadrate areas of the palatoquadrate contribute to this dorsoposterior flange (Fig. 55) which fuses with the inner surfaces of the preopercular and quadratojugal. This intimate contact of the palatoquadrate with the preopercular and quadratojugal dorsally and the maxilla ventrally, together with the strongly overlapping sutures between the maxilla, preopercular and quadratojugal, produces a rigid cheek unit (Gardiner 1967).

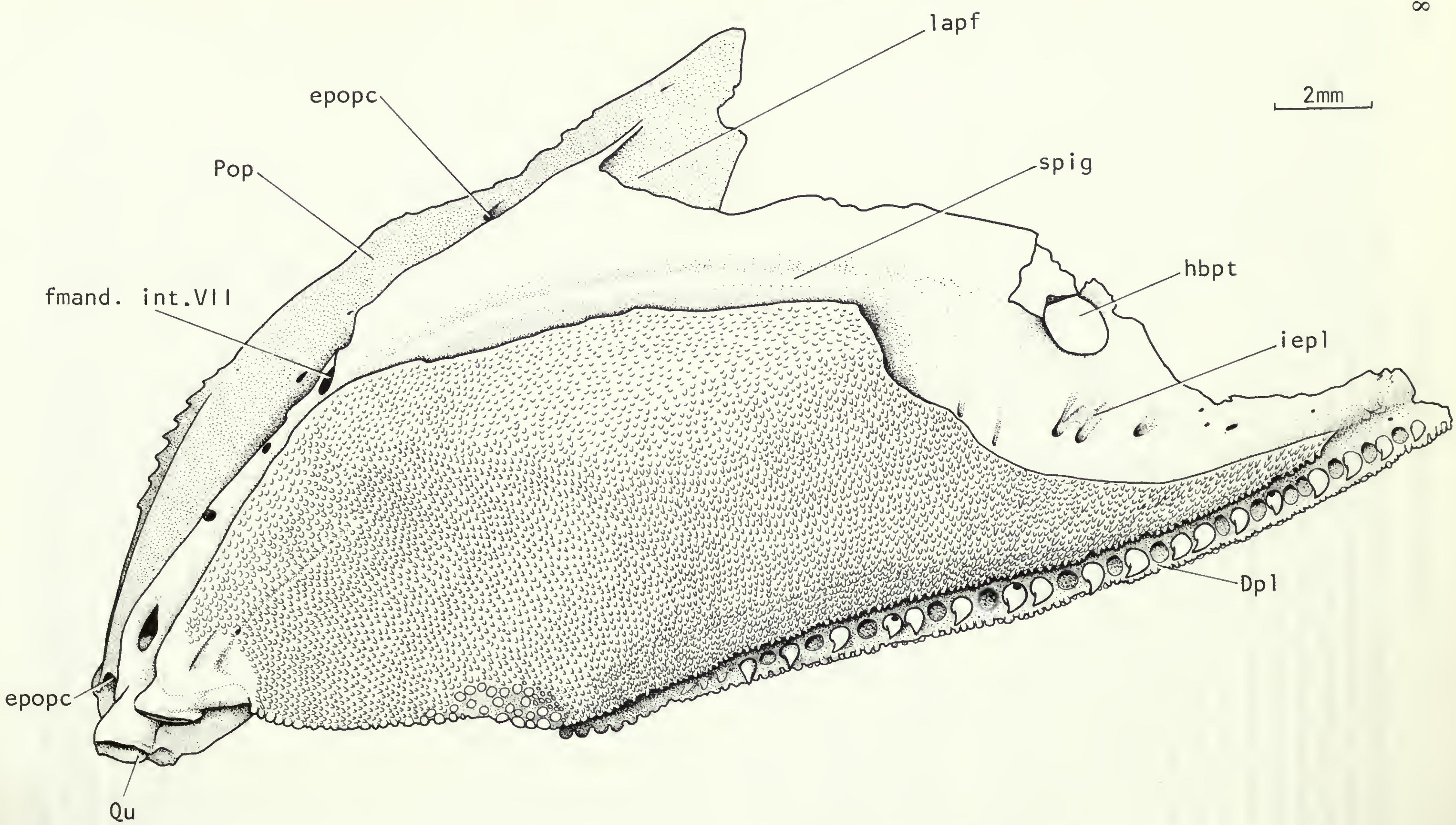
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Fig. 58 *Moythomasia durgaringa* Gardiner & Bartram. Left palatoquadrate and associated dermal bones in mesial view, from BMNH P.53221.

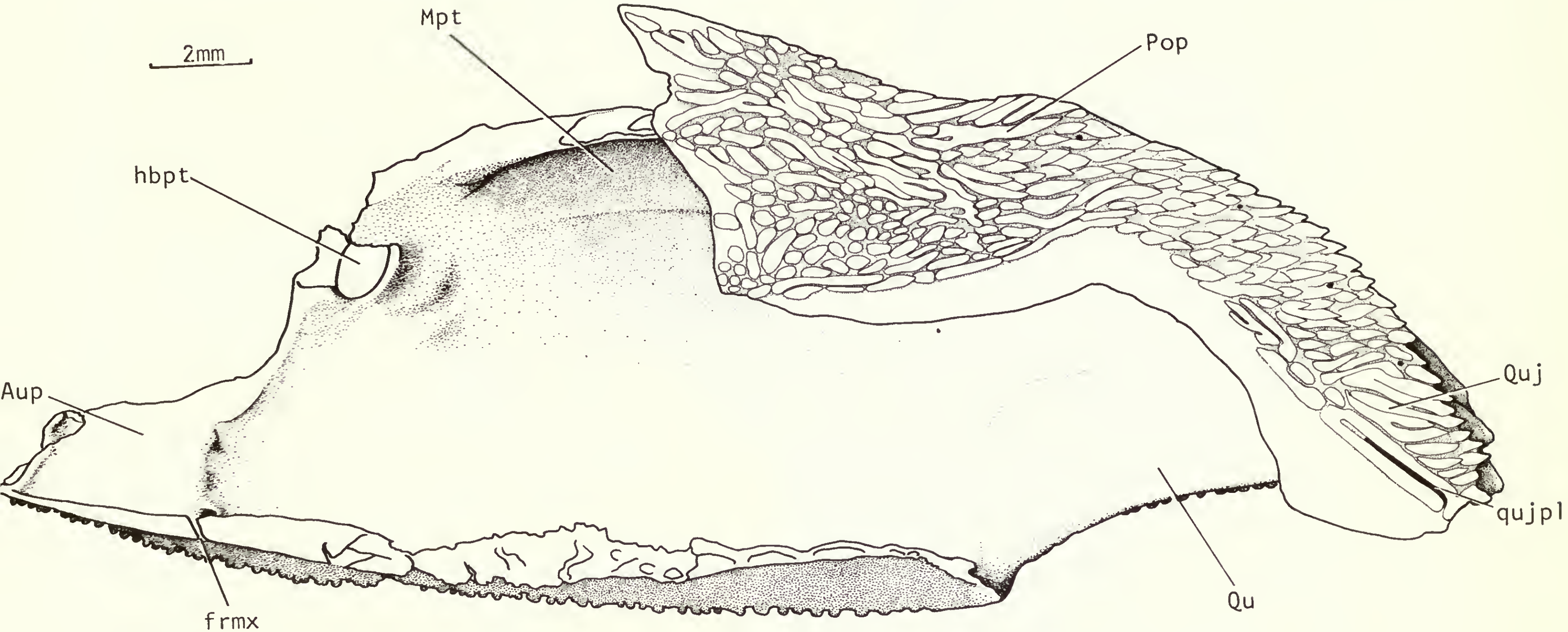
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Fig. 59 *Moythomasia durgaringa* Gardiner & Bartram. Left palatoquadrate, preopercular and quadratojugal in lateral view, from BMNH P.53221.

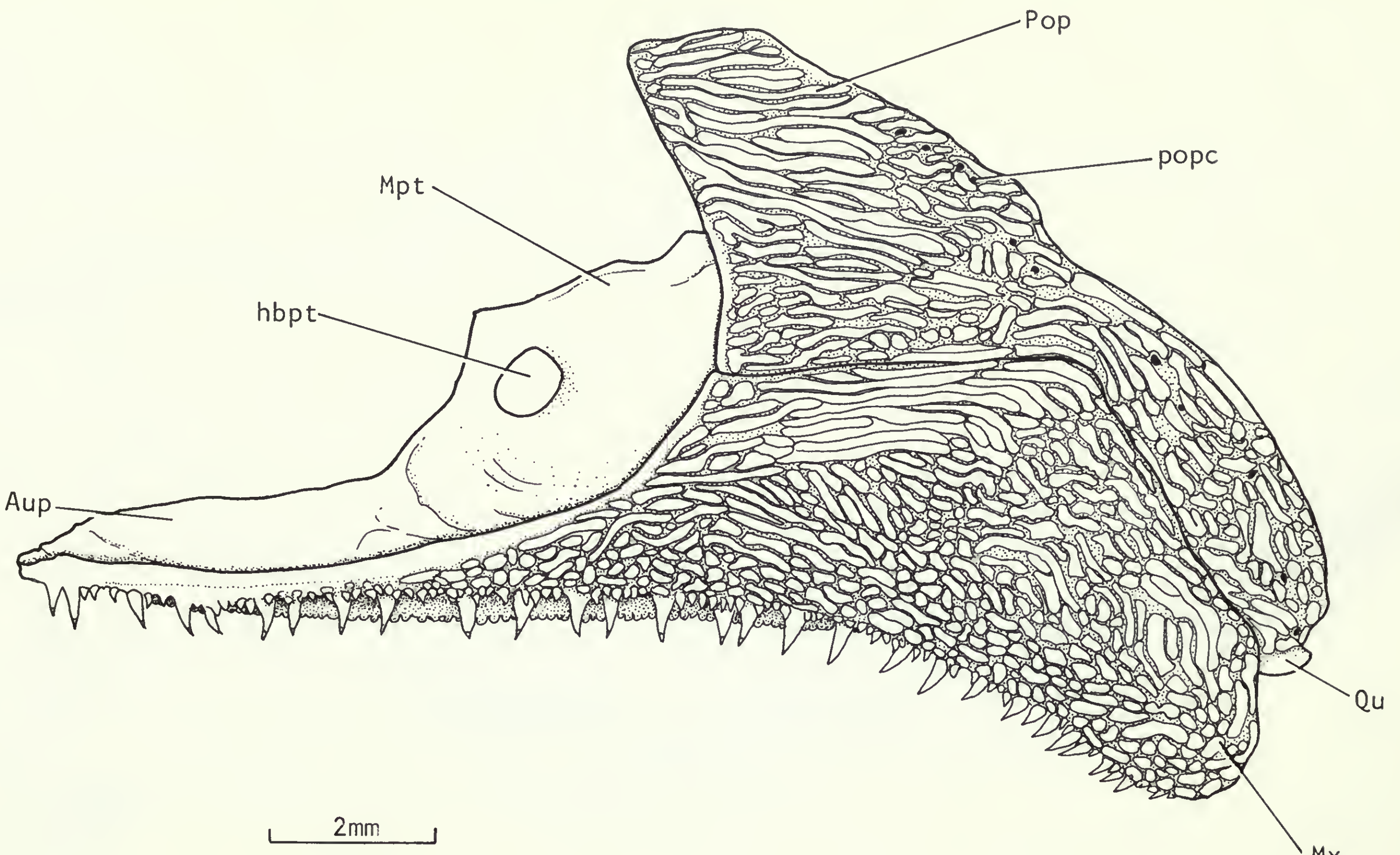
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Fig. 60 *Mimia toombsi* Gardiner & Bartram. Left palatoquadrate and associated dermal bones in lateral view, from BMNH P.56498.

The quadratojugal is overlapped dorsally by the preopercular and anteriorly by the maxilla and only a small portion of its surface is ornamented (Fig. 63). The radiation centre lies immediately anterior to the exposed, ornamented area beneath the pit-line. The quadratojugal pit-line, although short, is about the same length as the vertical pit-line and has at least three nerve foramina serving it.

The infraorbital series comprises three bones, the dermosphenotic, jugal and lachrymal. The dermosphenotic is considered here with the other cheek bones because it is in series with the infraorbital bones and is loosely attached or hinged to the skull roof.

The dermosphenotic is triangular in shape, sits over the top of the postorbital process and forms the anterolateral margin of the spiracular opening. The radiation centre is in the posterior third of the bone near its dorsal margin. The centre is pierced by the infraorbital canal which traverses it in a vertical direction. The infraorbital canal passes into the intertemporal anterior to the spiracular opening. A branch of the infraorbital canal passes anteriorly within the dermosphenotic to terminate blindly before reaching the anterior end of the bone. Ventrally the dermosphenotic is overlapped to a small degree by the anterodorsal margin of the jugal; anteriorly it may just make contact with the nasal and dorsally it contacts the frontal and intertemporal, resting on a ledge formed by the neurocranium. In some specimens it may also meet the anterior end of the supratemporal.

The jugal is the largest element of the infraorbital series. It has a convex posteroventral margin which overlaps the concave anterodorsal margins of the preopercular and maxilla. The course of the infraorbital canal changes from nearly vertical to nearly horizontal within the bone, the change of direction marking the radiation centre.

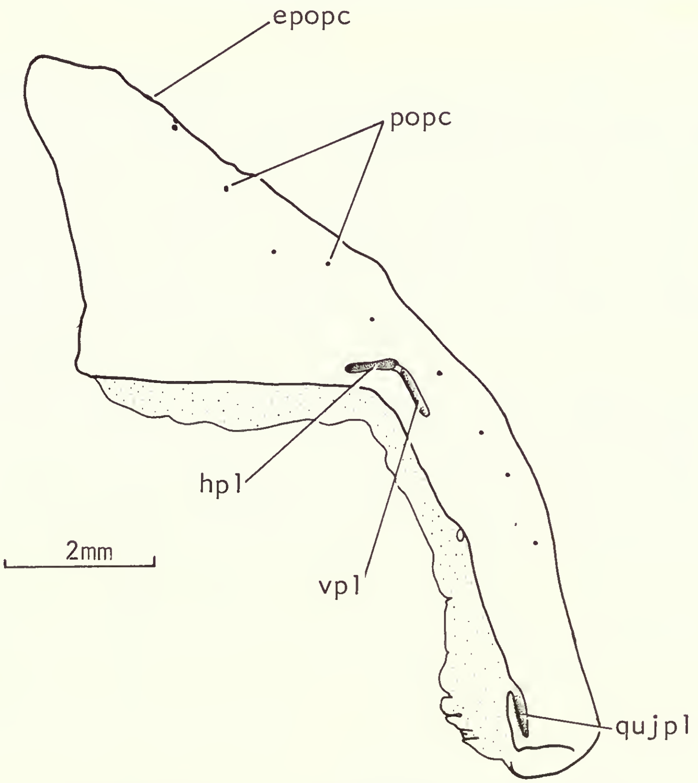


Fig. 61 *Mimia toombsi* Gardiner & Bartram. Sketch restoration of left preopercular and quadratojugal in lateral view, to show pit-lines.

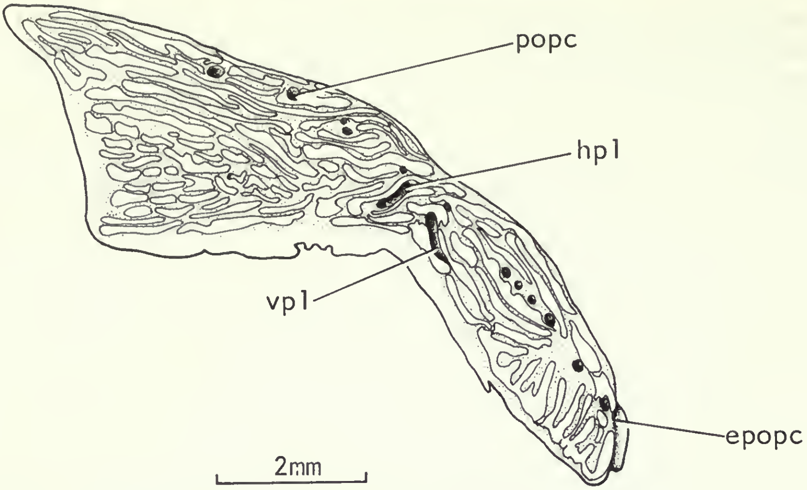


Fig. 62 *Mimia toombsi* Gardiner & Bartram. Left preopercular in lateral view, from BMNH P.56473.

The lachrymal is a short, thin ossification tapering to a point anteriorly. Posteriorly it overlaps the jugal while anteriorly it is overlapped by the premaxilla. The infraorbital sensory canals runs the length of the bone and the centre of radiation lies near the posterior margin. The external openings of the sensory canal lie along its ventral margin.

Moythomasia durgaringa

The palatoquadrate in *Moythomasia* differs in proportions from that of *Mimia*. It has a much longer post-basipterygoid portion and a correspondingly shorter and stouter anterior section. In shape it more nearly resembles that of *Cheirolepis* (Pearson & Westoll 1979: figs 7, 8) than any other described palaeoniscid. In all specimens the palatoquadrate is a single ossification and it is difficult to detect individual ossification centres. The anterior end, which turns inwards to articulate with the lateral ethmoid, is much broader than in *Mimia*, as is the facet on the lateral ethmoid. The whole of the ventral margin in front of the adductor fossa is produced laterally into a flattened flange (Fig. 59) which is intimately attached to the inner surface of the maxilla above the horizontal longitudinal lamina (hll, Fig. 67). Anteriorly this flange is pierced by one or more nerve foramina (frmx, Fig. 59) for branches of the maxillary nerve. As in *Mimia* there is a circular hole in the anterior dorsal margin (hbpt, Fig. 59) to accommodate the basipterygoid process. Beneath the hole on the medial surface of the palatoquadrate are several dorsally-directed pits (iepl, Fig. 58). By analogy with *Polypterus* these are presumed to have been insertion points for the ethmopalatine ligament (Allis 1922: 244). The posterolateral face of the palatoquadrate forms a broad flange which is in intimate contact with the preopercular and quadratojugal. This flange is pierced in its ventral half by four foramina. The dorsalmost of these foramina served for the entrance of the internal mandibular branch of the facial nerve and the ventralmost for its exit.

Like the cartilage bones, the dermal toothplates on the medial surface are ossified throughout as one bone. The toothplate is more extensive than in *Mimia* and forms much of the margin to the spiracular groove.

Laterally the dermopalatines are covered by small rounded teeth similar to those on the ventral ectopterygoid region. Medial to these is a series of much larger, pointed teeth, which show a similar replacement sequence to those on the maxilla and dentary. A well-marked groove separates this tooth row from the entopterygoid.

The maxilla has a shorter but much stouter postorbital portion than in *Mimia*. The teeth likewise are much stouter and less needle-like. At the centre of radiation of the maxilla several

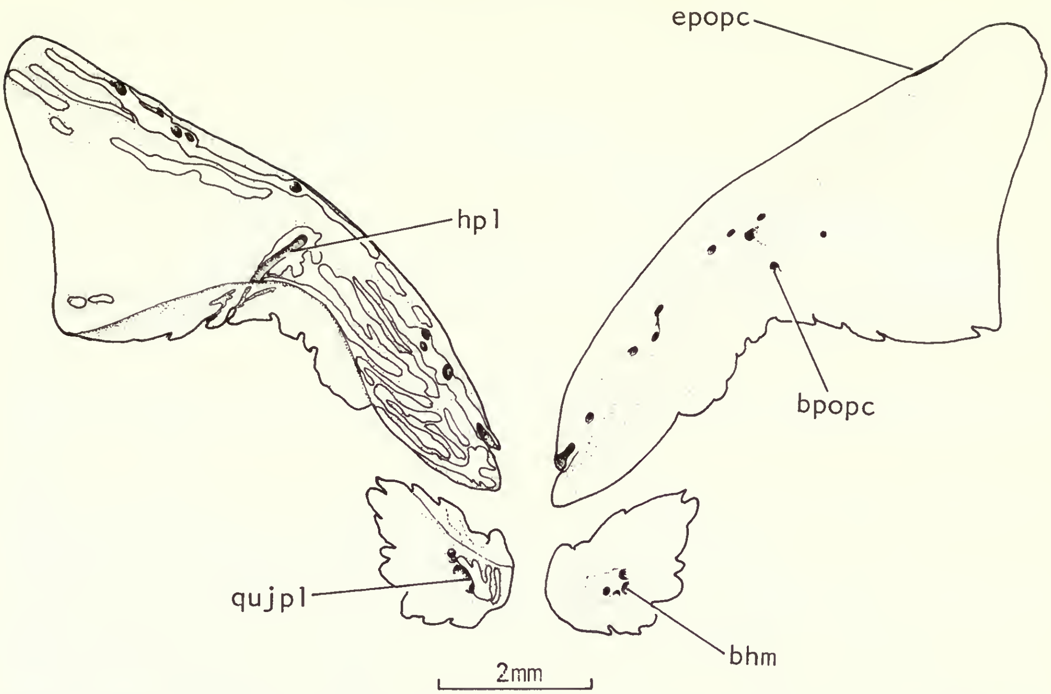


Fig. 63 *Mimia toombsi* Gardiner & Bartram. Left preopercular and quadratojugal in lateral (left) and medial views, from BMNH P.56484.

nerve foramina pass into the medial surface (bhm, Fig. 67), whereas externally a corresponding series of pits presumably housed the neuromasts of the anterior part of the horizontal pit-line (hpl, Fig. 66). An anterior continuation of the horizontal pit-line is also found on the maxilla of *Polypterus* (Jarvik 1947: fig. 1) and *Pteronisculus* (Nielsen 1942: pl. 9, fig. 1).

The preopercular is not so expanded dorsally as that of *Mimia* and the preopercular canal exits two-thirds of the way along the posterodorsal margin (epopc, Fig. 58).

The quadratojugal is stout and triangular and the pit-line makes a long slanting groove on its surface. Medially three nerve foramina transmitted fine branches of the mandibular nerve to the line.

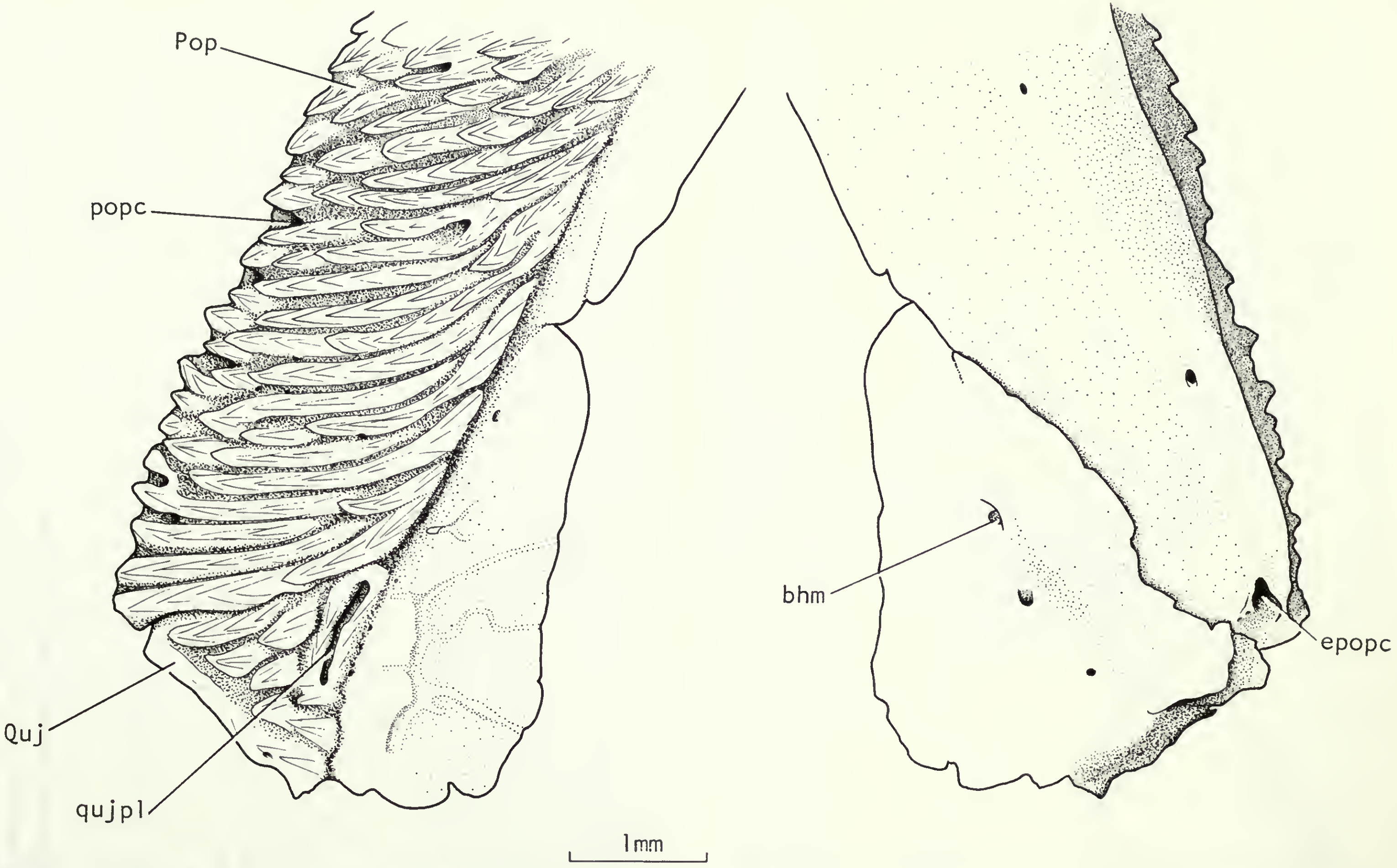
The dermosphenotic is less extensive both anteriorly and ventrally than in *Mimia*. Anteriorly it tapers to a point and scarcely contacts the nasal. Posteroventrally it is overlapped by the jugal.

The jugal is more strongly convex posteriorly than in *Mimia* and the infraorbital canal opens by two sets of pores ventrally rather than a dorsal suite of pores as in *Mimia*.

The lachrymal is very different in shape from that of *Mimia*; much broader, and bifurcated anteriorly at the point of the exit of the infraorbital canal. Posteriorly the lachrymal overlaps the jugal, but anteriorly it overlaps the premaxilla. Anteroventrally the ornament closely resembles that on the ventral edge of the maxilla. A similar ornamentation is found on the posteroventral margin of the premaxilla and rostral. The infraorbital sensory canal enters and leaves the lachrymal through dorsally-directed pores (inc, Fig. 74). Beneath the canal several pores pass right through the bone (p, Fig. 74), as they do through the premaxilla.

Palatoquadrate: summary and discussion

1. *Palatoquadrate commissure and vomer*. In the ontogenetic development of actinopterygians and dipnoans the anterior ends of the palatoquadrates are joined by a blastema both to one another and to the overlying trabeculae (Holmgren 1943, Bertmar 1966). This blastema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popc
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Fig. 64 *Moythomasia durgaringa* Gardiner & Bartram. Ventral end of right preopercular and quadratojugal in lateral (left) and medial views, from BMNH P.56502.

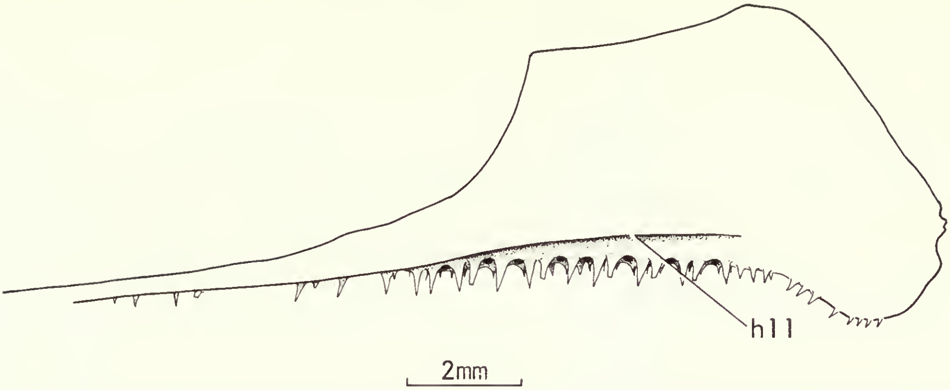

Fig. 65 *Mimia toombsi* Gardiner & Bartram. Right maxilla in medial view, from BMNH P.56486.

(intermediating body or symphysial portion) then chondrifies to form the palatoquadrate commissure and is incorporated in the floor of the ethmoid region.

In *Amia, Lepisosteus* and teleosts (Holmgren 1943, Bertmar 1959) the primary palatoquadrate commissure chondrifies as a single unit which later fuses into the ethmoid plate. In *Acipenser* (Holmgren 1943: figs 26, 28) this primary commissure is possibly represented by the so-called tentacle blastemas.

In selachians (Holmgren 1940), although there is always an early, mesenchymatic, frontal connection between the palatoquadrates and the trabeculae, there is never an intermediating body or symphysial portion joining the palatoquadrates to the floor of the ethmoid region. Instead, somewhat later in development, after the formation of the basal (orbital) processes, the anterior ends of the palatoquadrates grow forwards and inwards to meet in the mid-line, forming a symphysis (see under anterior articulation, p. 297) which ventrally supports teeth. This symphysis is found in all extant selachians. A similar shark-like palatoquadrate commissure is seen in *Acipenser* (where it must be considered to be secondary, not primitive; see below under anterior articulation), and in the acanthodian *Ptomacanthus* (Miles 1973*b*: pl. 6) and possibly in the placoderm *Jagorina* (Stensiö 1969: 71).

In osteichthyans the vomer develops beneath the primary palatoquadrate commissure and therefore lies in sequence with the dermopalatines. From this it follows that the dermopalatine–vomer sequence is homologous throughout the osteichthyans.

The vomer is paired in *Mimia, Moythomasia, Boreosomus*, saurichthyids (Gardiner 1960: fig. 21), *'Aspidorhynchus', Lepisosteus*, caturids (Gardiner 1960: fig. 36), parasemionotids (Patterson 1975: figs 30, 41), *Amia*, pachycormids (Lehman 1949: fig. 4; Patterson 1975: 513), and the teleosts *Hiodon* and *Osmerus* (Patterson 1975: 513).

There is a median vomer in living chondrosteans (toothless in *Polyodon, Acipenser* and *Scaphirhynchus*, Sewertzoff 1926: figs 3, 4, 39, the so-called median basirostral), *Bobasatrania* (Nielsen 1952: 199), in the semionotids *Dapedium* and *Lepidotes* (Gardiner 1960: 322), in pycnodonts, leptolepids and the majority of teleosts (Patterson 1975: 515). In the last group the vomer fuses with the ventral ethmoid during ontogeny. There is usually good evidence in teleostean embryology for the paired origin of the vomer (de Beer 1937: 126, 130, 159).

A vomer is absent in *Pteronisculus, Australosomus* and adult specimens of *Polypterus*. Nevertheless a binary primordium has been described in the 30 mm stage of *Polypterus bichir* by Holmgren & Stensiö (1936: 397), and a median vomer in the 24 mm, 32 mm and 125 mm stages of *Polypterus* by Pehrson (1947: 448).

The vomer is paired in actinistians (*Whiteia, Latimeria*, Millot & Anthony 1958), porolepids (*Porolepis, Glyptolepis, Holoptychius*, Jarvik 1972: pls 3, 17, 25) and osteolepids (*Megalichthys, Ectosteorhachis*, Jarvik 1966; *Eusthenopteron*, Jarvik 1942: fig. 56). In dipnoans it may be paired or median. The vomer is paired in *Uranolophus* (Denison 1968), *Dipnorhynchus* (anterior

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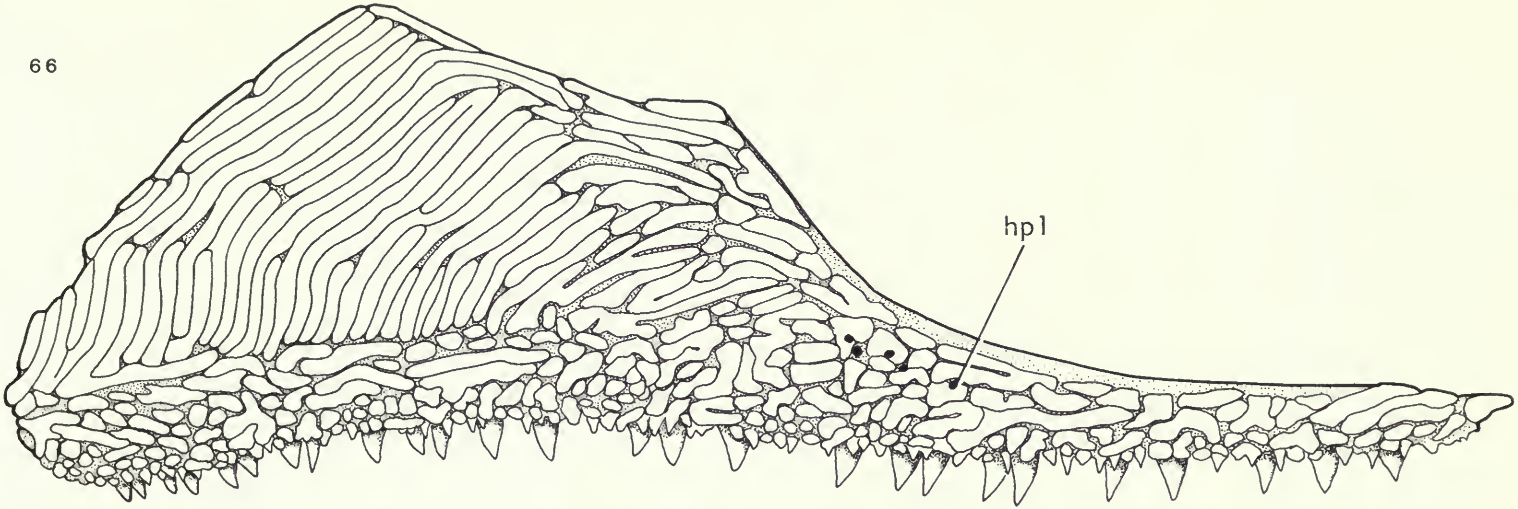

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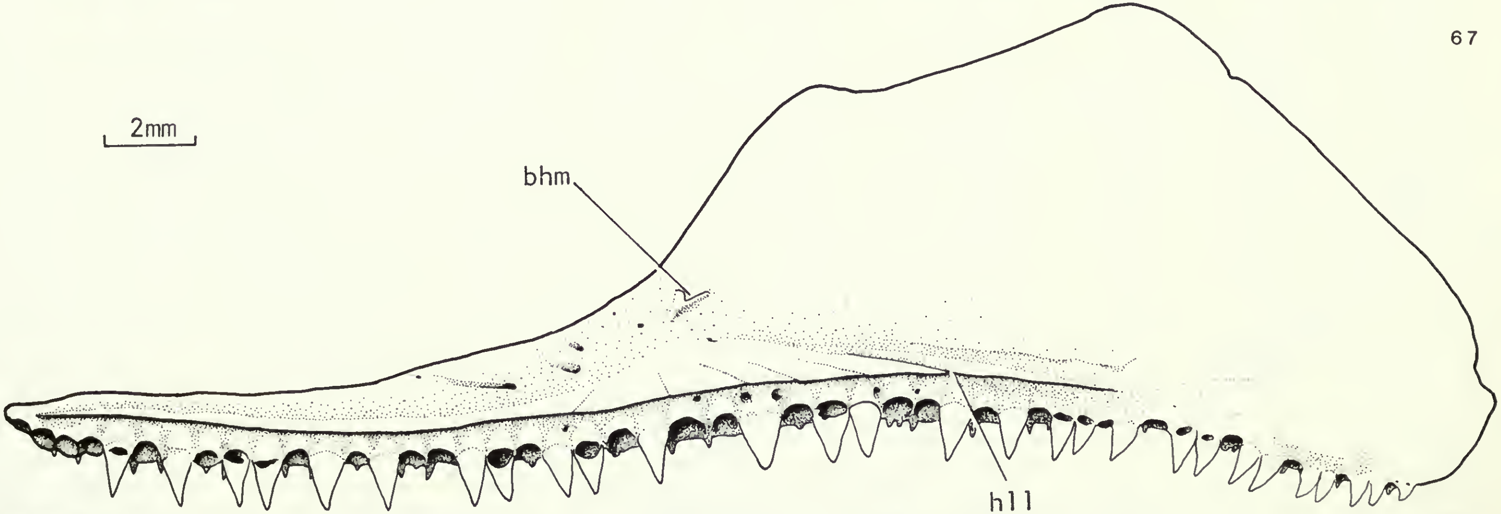

Figs 66–67 *Moythomasia durgaringa* Gardiner & Bartram. Right maxilla, from BMNH P.53221. Fig. 66, lateral view. Fig. 67, medial view.

pterygoids of Thomson & Campbell 1971), *Griphognathus* (dermopalatinum of Schultze 1969: fig. 4; dermopalatine 1 of Miles 1977: fig. 57), *Ceratodus, Sagenodus, Uronemus* (Miles 1977: 175), *Conchopoma* (Schultze 1975), *Gnathorhiza* (Berman 1968), *Monongahela* (Lund 1970), *Neoceratodus, Lepidosiren* and *Protopterus* (Miles 1977: 175). There is a median vomer in *Chirodipterus, Holodipterus* (Miles 1977: figs 67, 87) and *Scaumenacia* (Jarvik 1967*a*: pl. 6).

The vomer is paired in Recent Amphibia, but median in Recent chelonians, lacertilians, birds and monotremes. However, in the development of these choanates with a median vomer there is often evidence of paired origin (de Beer 1937: 434).

In summary, the osteichthyan vomer is primitively a paired bone which fuses into a median element in actinopterygians, dipnoans, lacertilians, chelonians, birds and monotremes. In actinopterygians this fusion has occurred independently on at least five occasions, in *Polypterus*, in Recent chondrosteans, in *Bobasatrania*, in semionotids and pycnodonts, and in teleosts.

2. *Anterior articulation*. In actinopterygian ontogeny, after the separation of the intermediating body, the anterior ends of the palatoquadrates (the so-called pterygoid processes) come into close contact with the ethmoid region (postnasal wall). Subsequently an articulation develops between the anterior end of the palatoquadrate (autopalatine) and the lateral ethmoid, the rostro-palatine articulation. An anterior articulation is found in most actinopterygians, with the exception of Recent and fossil chondrosteans where in *Acipenser* and *Polyodon* the two palatoquadrate bars meet in the mid-line forming a symphysis well below the ethmoid region. In *Acipenser*, however, they are still connected with this region by a ligament (Holmgren 1943: fig. 27), much as in *Carcharhinus*. The palatoquadrates are separate and distinct in *Chondrosteus* (BMNH P.2048) and meet in the mid-line. The rostro-palatine articulation is single in primitive actinopterygians (*Mimia, Moythomasia, Polypterus*), *Amia* and halecomorphs, but in teleosts it is often double (*Salmo*, etc.; Gardiner 1973: 119).

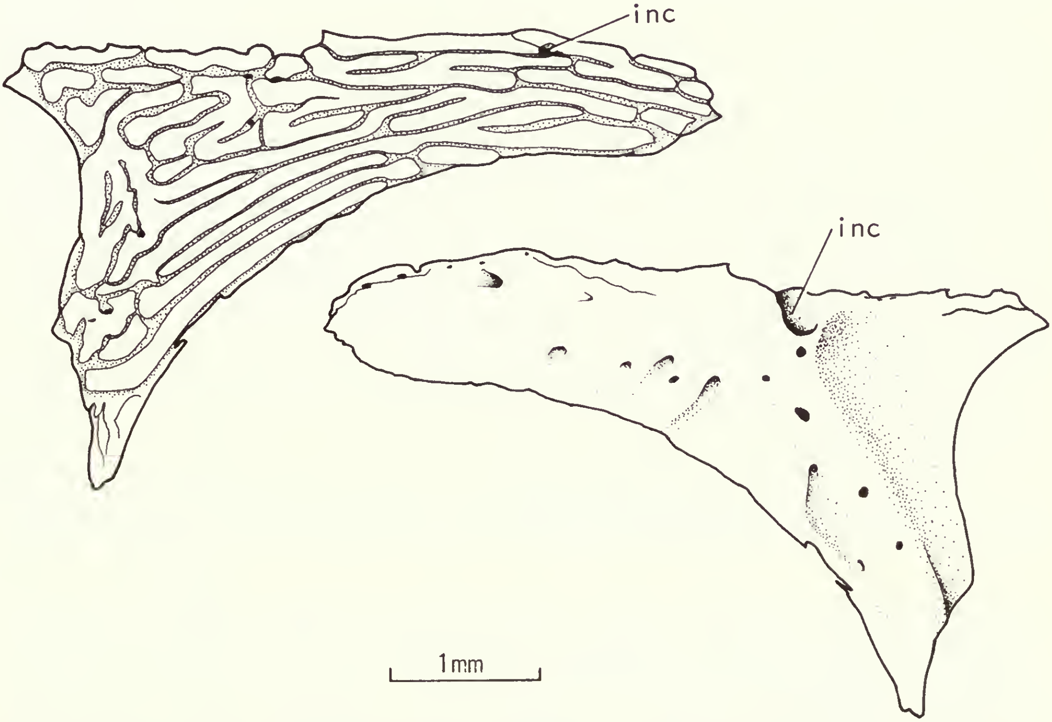

Fig. 68 *Mimia toombsi* Gardiner & Bartram. Right dermosphenotic in lateral (above) and medial views, from BMNH P.56483.

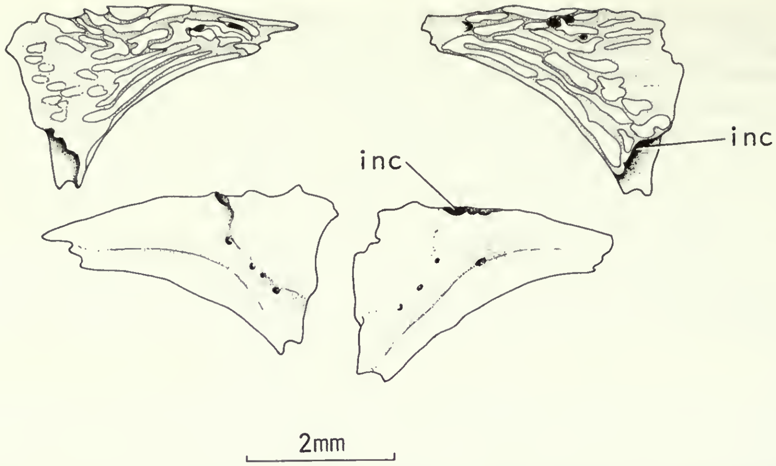

Fig. 69 *Moythomasia durgaringa* Gardiner & Bartram. Dermosphenotics in lateral (above) and medial views, from BMNH P.53255. The right dermosphenotic is on the left.

A similar, single rostro-palatine articulation is found in actinistians (*Latimeria, Rhabdoderma, Macropoma, Undina*), but in porolepids (*Glyptolepis* Jarvik 1972: fig. 25) and *Youngolepis* (Chang 1982) this articulation is supported by additional articulatory facets or points of fusion (Jarvik 1972: 71) between the autopalatine and suborbital shelf. In *Eusthenopteron* the rostro-palatine articulation is said to be double (Jarvik 1942: figs 48, 50, 54, art m, art l) but in an acid-prepared specimen (BMNH P.60310, Rosen *et al.* 1981) it is single. This articulation is supported by a more medial articulation between a dorsomedial process of the autopalatine and the orbital wall (suborbital shelf) (Jarvik 1954: figs 24, 40, pr.dm) and by the head of the dermopalatine which articulates with the vomer (Rosen *et al.* 1981: figs 13, 14). In *Polypterus* the primary rostro-palatine articulation is also supported by articulations of the dermopalatines.

In placoderms a single rostro-palatine articulation has been recorded in *Holonema* (Miles 1971*b*) and *Dicksonosteus* (Goujet 1975: fig. 4), and a double articulation in *Ctenurella* (Ørvig 1960: pl. 29, fig. 1; Miles & Young 1977: fig. 27D) and *Buchanosteus* (Young 1979: fig. 15). In acanthodians an anterior articulation is unknown and in the Permian *Acanthodes* (Miles 1965: fig. 1) the palatoquadrates extend forward only as far as the posterior rim of the orbit. Here there is no possibility of an anterior articulation (rostro-palatine), or of an anterior symphysis as in *Ptomacanthus* (Miles 1973*b*: pl. 6), because the palatine ossification has an unbroken covering of perichondral bone (Reis 1896). It cannot have had an unossified palatine process as proposed by Holmgren (1942: 138).

The palatoquadrate always meets its fellow in the mid-line in Recent selachians and may have a ligamentous attachment with the ethmoid region, as in *Carcharhinus*, or a sliding articulation, as in *Chlamydoselachus*.

On this evidence an anterior articulation cannot be primitive for gnathostomes. However, there is little doubt that a single anterior articulation is the primitive osteichthyan condition, with the autopalatine meeting the lateral ethmoid. The articulation of the autopalatine with the postnasal wall is considered synapomorphous for placoderms plus osteichthyans.

3. *Otic process and palatobasal articulation*. The posterodorsal expansion of the palatoquadrate is referred to as the otic process. This process is frequently single as in many chondrichthyans (*Cladoselache, Cladodus, Xenacanthus, Squalus, Heterodontus*), placoderms (*Ctenurella, Buchanosteus*, Young 1979: figs 2, 12), acanthodians (*Climatius*, Miles 1973*b*: fig. 8), actinopterygians (*Polypterus, Polyodon*) and actinistians (*Rhabdoderma, Wimania, Latimeria*). The otic process may be notched for the maxillary and mandibular branches of the Vth nerve

(*Chlamydoselachus, Mustelus, Acanthodes, Amia, Eusthenopteron, Porolepis*). When notched the anterior division of the otic process is referred to either as the basal (orbital) process (selachians, actinopterygians) or as the ascending process (actinistians, rhipidistians). The single dorsal process of tetrapods is also referred to as the ascending process. The connection which develops between the anteroventral region of the otic process (so-called basal process) and the basipterygoid process is referred to as the palatobasal articulation.

The basipterygoid process is typically developed in osteichthyans, but it is also recognizable in many selachians where it forms part of the subocular shelf as in *Heptranchias*, and in *Squalus* (Jollie 1971) where it arises from the site of the polar cartilages.

In living actinopterygians the contact between the palatoquadrate and basipterygoid processes is only to be seen in *Lepisosteus* (Hammarberg 1937: fig. 9) and *Acipenser* (Holmgren 1943: 30). In the latter a distinct blastema joins the palatoquadrate with the trabecula (Holmgren 1943: figs 26, 27), and this later transforms into a ligament which according to Bugajew (1929) may chondrify. However, no such chondrification was observed by de Beer (1937: 91), Edgeworth (1935) or Holmgren (1943: fig. 27).

In *Polypterus* (Budgett 1901), *Amia* and *Salmo* (Holmgren 1943: 37, 40) the basipterygoid process is not developed. Nevertheless in the development of *Amia* and *Salmo* the palatoquadrate is connected with the trabecula by means of a thin membrane along its upper border. In *Pteronisculus* there is either a tongue-like process of the metapterygoid (in part supported by a corresponding tongue on the entopterygoid; Nielsen 1942: figs 34–37), which articulates with the basipterygoid process, or there is a hole in the metapterygoid at the base of the otic process (Lehman 1952: fig. 53), as in *Mimia, Moythomasia* and *Kentuckia* (Rayner 1951: fig. 3), through which the basipterygoid process presumably slid during lateral movements of the palatoquadrate. There is an articular fossa at the base of the otic process in *Boreosomus* (Nielsen 1942: fig. 70), while in *Australosomus* (Nielsen 1949: fig. 28) the anterior edge of the otic process is produced into a prominent, medially-directed process. The loss of the palatobasal articulation in *Polypterus, Amia* and teleosts may be directly correlated with the loss of the endochondral basipterygoid process in these fishes and in *Polypterus* with the articulation of the entopterygoid with the parasphenoid.

In Devonian actinistians (*Nesides, Diplocercides*) the basipterygoid process articulates with the inside of the metapterygoid near the base of the otic process, where there is a marked articular fossa (Bjerring 1977: fig. 28F), but as in later actinopterygians the basipterygoid process is missing in *Macropoma, Rhabdoderma* and *Latimeria*.

In the porolepid *Glyptolepis* (Jarvik 1972: 58) and in the osteolepids *Megalichthys* and *Eusthenopteron* (Jarvik 1954: figs 16, 22B) the condition is much as in *Nesides*, with a well-developed basipterygoid process articulating with the base of the otic process; the latter extends almost to the underside of the fronto-ethmoidal shield and there articulates with the neurocranium.

In later acanthodians such as *Acanthodes* (Miles 1965: 238) there is a distinct notch in the anterior margin of the otic process and the anterior process (basal process) articulated with the basipterygoid process. The only difference from the condition in osteichthyans is that the anterior process is ossified by the autopalatine and not the metapterygoid.

In ptyctodont placoderms the otic process has a grooved medial surface for a presumed articulation with a basipterygoid process. A palatobasal articulation has also been described at the base of the otic process in arthrodires (*Buchanosteus*, Young 1979: figs 2, 12).

In dipnoans the base of the otic process fuses with the trabecula (de Beer 1937: 172) and its top fuses with the orbital wall during development. A similar fusion occurs in holocephalans, anurans and urodeles.

In the fossil amphibian *Palaeoherpeton* the otic process is prominent and is ossified by the epipterygoid. Ventrally on its inner surface there is a distinct roughened recess (Panchen 1964: fig. 5), where it was probably in cartilaginous (immovable) contact with the basipterygoid process. In monotremes the otic process is ossified by the alisphenoid (Presley & Steel 1976) and consequently this bone may be homologous with the osteichthyan metapterygoid and the amphibian and 'reptilian' epipterygoid (Broom 1914).

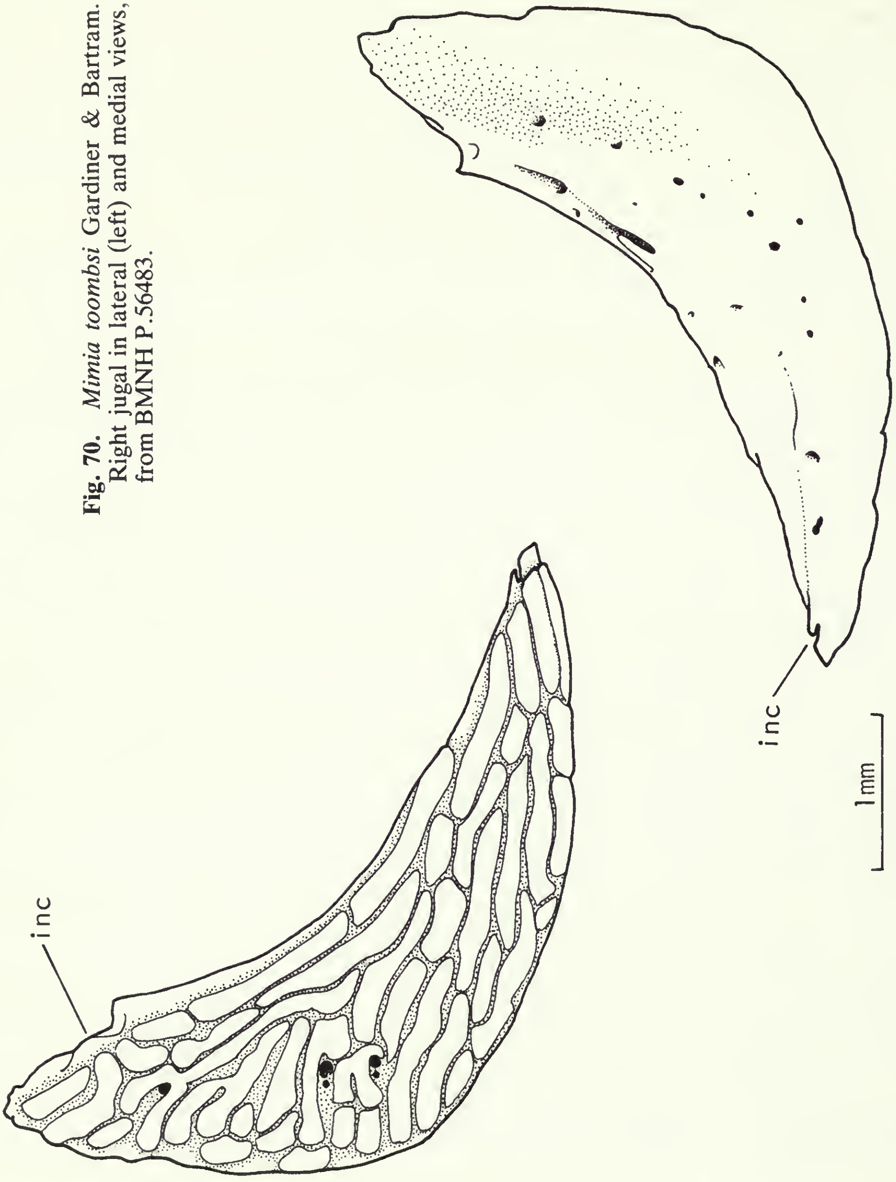

Fig. 70. *Mimia toombsi* Gardiner & Bartram. Right jugal in lateral (left) and medial views, from BMNH P.56483.

The palatoquadrate and Meckel's cartilages are generally regarded as the epimandibular and ceratomandibular elements respectively, with the anterior division of the otic process (basal process) often being regarded as dorsalmost elements of a branchial arch (Huxley 1876; de Beer 1937). Sewertzoff & Disler (1924) suggested that the basal process (anterior otic process) is serially homologous with the pharyngobranchials of the succeeding visceral arches; Holmgren (1943: 64) and Bertmar (1959) homologized it with the actinopterygian suprapharyngobranchial. The evidence for considering the anterior division of the otic process a pharyngomandibular rests on the claims of Sewertzoff & Disler (1924) that there is an independent nodule of cartilage (or prochondral rudiment) which fuses to the medial surface of the basal process in *Squalus, Scyllium, Mustelus* and *Somniosus*, and on the presence of separate cartilages in the anterior region of the palatoquadrate in *Scaphirhynchus* and *Acipenser* (Bugajew 1929). However, de Beer found no evidence of this cartilage in any of his specimens of *Squalus* (1937: pls 11, 12) or *Scyllium* (1937: pls 13, 14, 15), nor did Holmgren (1940) find any trace of a separate nodule in his exhaustive study of the embryology of *Squalus* and *Etmopterus*. Holmgren concluded (1943: 64) that 'in Squaloid sharks the orbital process is formed in continuum with the palatoquadrate proper'. Nevertheless he found that in *Scyllium* (Holmgren 1940: 153; fig. 104) and *Mustelus* (1943: 53) the anterior division of the otic process (basal process) had a separate blastemic origin, although it subsequently chondrified in conjunction with the remainder of the palatoquadrate (1940: 164). The cartilages described by Ivanzoff (1887) in *Scaphirhynchus* and by Bugajew (1929: 98) in *Acipenser* lie in the connective tissue covering the basitrabecular process and thus do not appear to belong to the palatoquadrate. There is therefore no evidence in the development of the anterior division of the otic process (basal process) to support the theory that it is a pharyngomandibular. Moreover since suprapharyngobranchials appear to be an osteichthyan specialization (see p. 362) there is even less evidence for considering the anterior otic process to be a suprapharyngomandibular.

Unfortunately the situation is further complicated by the assumption of several workers (Holmgren 1943) that the anterior division of the otic process of actinopterygians is not homologous with the selachian anterior otic process and that neither is homologous with the choanate otic (ascending) process (Goodrich 1930: 413; de Beer 1937: 419). But the so-called ascending process which is presumed by Goodrich (1930: 413) and de Beer (1937: 420) to be present only in Dipnoi and tetrapods is no more than a dorsally extended otic process, much as in *Nesides* (Jarvik 1954: fig. 15), *Glyptolepis* (Jarvik 1972: fig. 25) and *Eusthenopteron* (Jarvik 1954: fig. 23B). In actinistians, porolepids and *Eusthenopteron* the top edge of the otic process articulates with the postorbital process (antotic process). In dipnoans and Recent amphibians the top of the process fuses with the neurocranium (orbital cartilage). From these comparisons it follows that both the single otic process and the palatobasal articulation may be regarded as primitive gnathosome characters. The palatoquadrates of *Ctenurella* and *Jagorina* suggest that the omega-shaped (Schaeffer 1975) palatoquadrates of other placoderms are derived.

4. *Otic process and prespiracular cartilage.* In both fossil and Recent selachians the otic process is prominent and in *'Cladodus', Xenacanthus, Tamiobatis* (Romer 1964), *Hybodus* (Maisey 1982, 1983), *Heptranchias* (Daniel 1934) and *Pseudocarcharias* (Compagno 1973: 20) it articulates with the postorbital process as in *Acanthodes*. In the majority of sharks the process does not articulate with the braincase (e.g., *Chlamydoselachus, Etmopterus, Isurus, Oxynotus, Scyliorhinus, Squalus*), and the otic process is missing in rays (e.g., *Raja*) and in *Urolophus* (Holmgren 1940: fig. 181).

Both de Beer (1937: 420) and Holmgren (1943: 61) believed that in many selachians (*Scyllium, Squalus*, etc.), the otic process becomes detached as the prespiracular cartilage (or spiracular rudiment). In the development of *Heterodontus, Raja, Urolophus* and *Etmopterus* Holmgren (1940; 1943: 60) has shown how the spiracular rudiment arises as a mesenchymatic lamella, partly attached to the margin of the palatoquadrate anterior to the spiracular canal. It subsequently contacts the postorbital process and fuses with it dorsally. Later that part of the rudiment in front of the spiracle chondrifies independently of the palatoquadrate, with which it loses contact, as the prespiracular cartilage. In *Etmopterus* Holmgren (1940: fig. 95) described

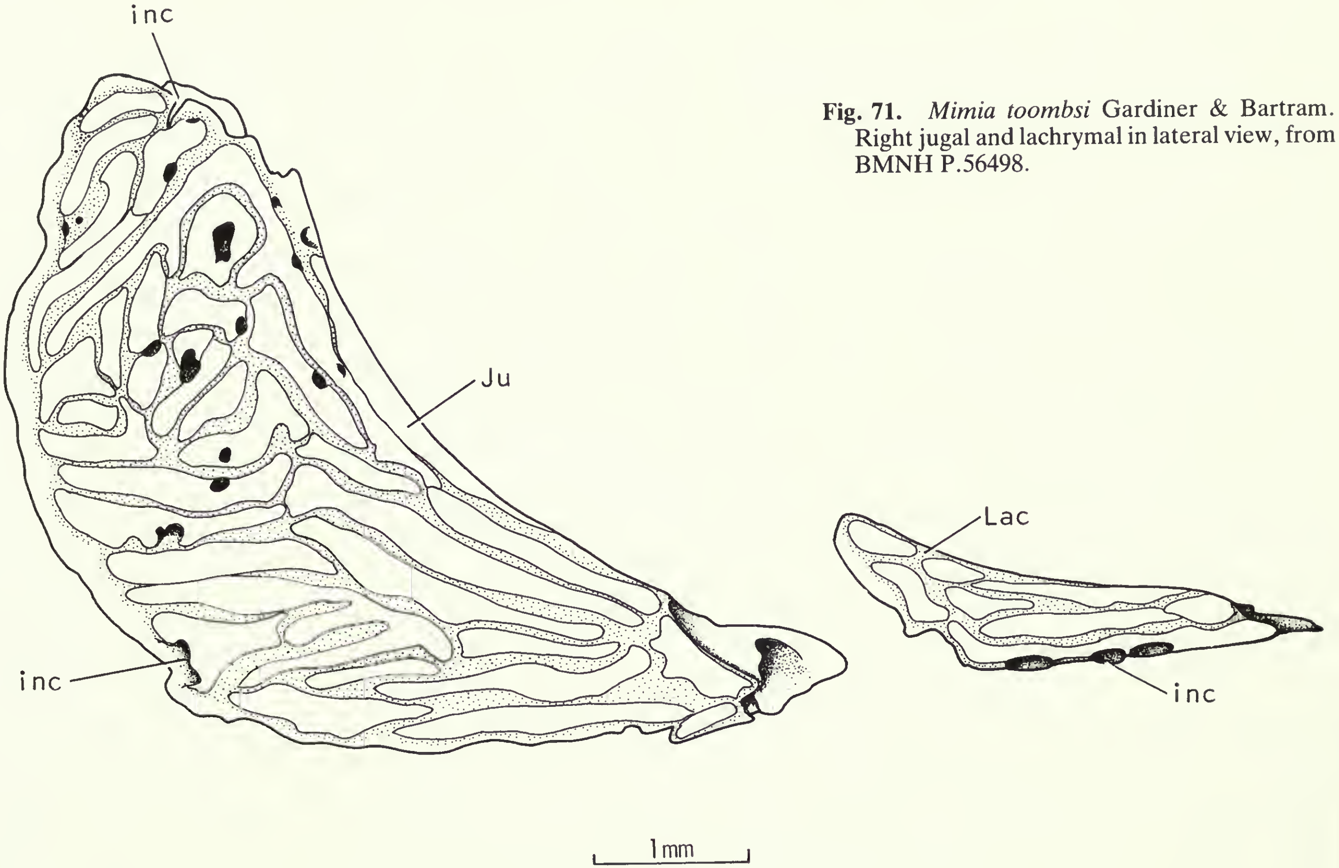
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Fig. 71. *Mimia toombsi* Gardiner & Bartram. Right jugal and lachrymal in lateral view, from BMNH P.56498.

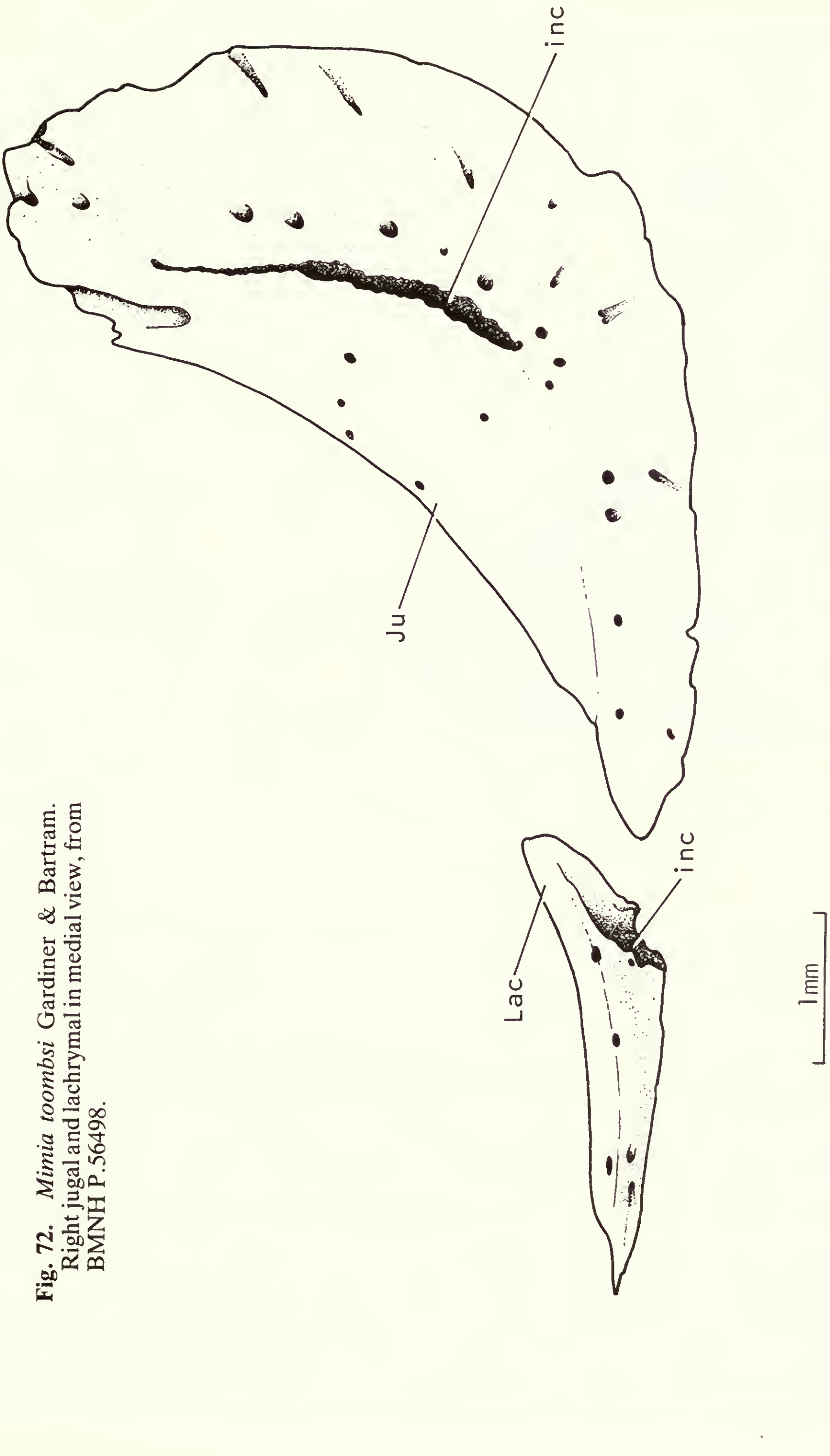
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Fig. 72. *Mimia toombsi* Gardiner & Bartram. Right jugal and lachrymal in medial view, from BMNH P.56498.

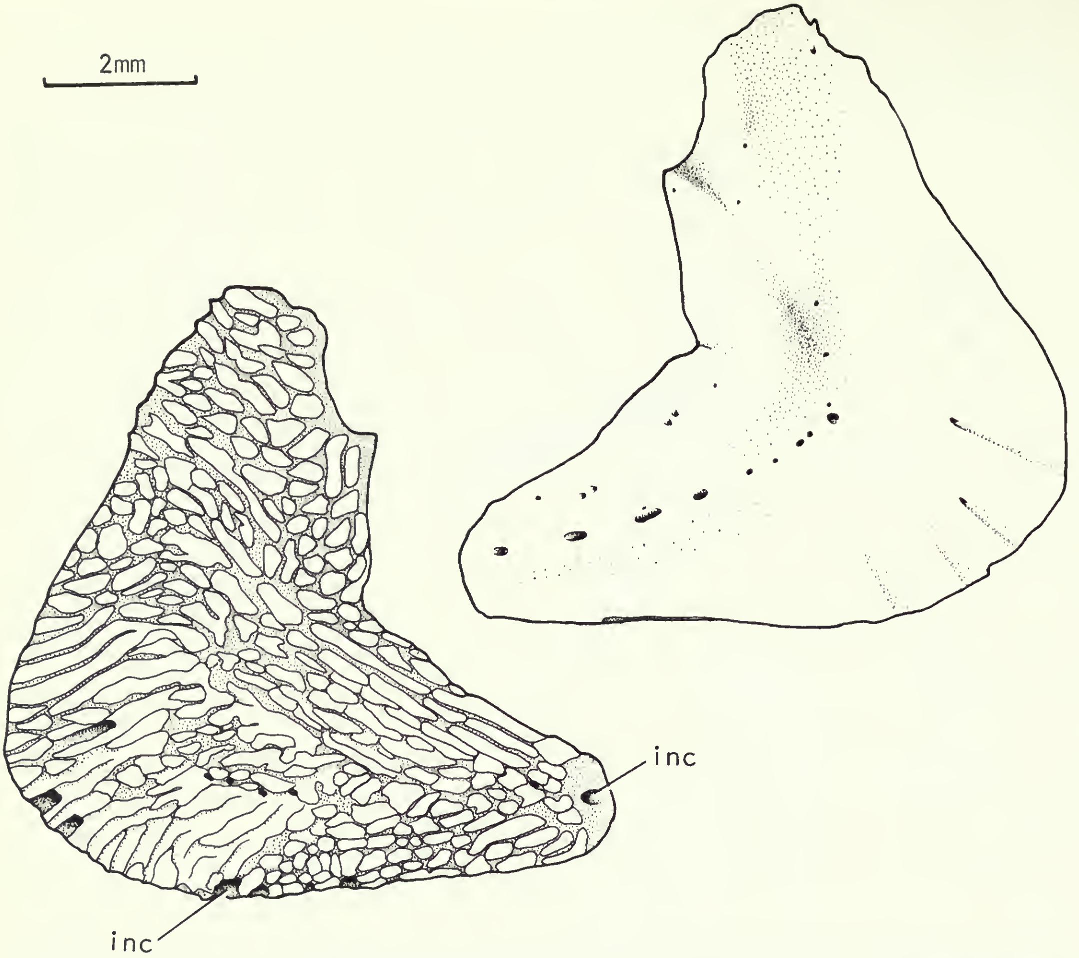

Fig. 73 *Moythomasia durgaringa* Gardiner & Bartram. Right jugal in lateral (left) and medial views, from BMNH P.53221.

both an otic process and a prespiracular cartilage and it became increasingly difficult to see how the prespiracular cartilage could be the homologue of the otic process. In order to resolve this apparent dilemma, Holmgren (1940: 140, 144; 1943: 56, 62) suggested that in *Etmopterus* the otic process was not homologous with that in some other selachians (notidanids), dipnoans and amphibians and that there were two distinct otic processes in sharks and rays, the processus oticus externus and the processus oticus internus. He showed that the processus oticus externus (1940: 140; 1943: 62) developed from the fusion of an extra palatoquadrate blastema with the palatoquadrate blastema, after which chondrification took place, while the processus oticus internus (1940: 131; 1943: 62) formed simultaneously as the lateral commissure. In 1940 Holmgren concluded that the otic process in *Etmopterus* was homologous with that in *Heptranchias*, but in 1943 he was so confused that he at first considered them not the same, then homologous and finally non-homologous all on the same page (p. 62). It is very difficult to comprehend the movements and fusions of the various cell masses associated with the development of the palatoquadrate in selachians as described by Holmgren (1940, 1943), but if we confine our attention to the cartilage it is remarkably similar to that in osteichthyans. Further, since the palatoquadrate and prespiracular cartilages always chondrify as separate structures there is no reason to believe the latter to be a detached otic process, especially when

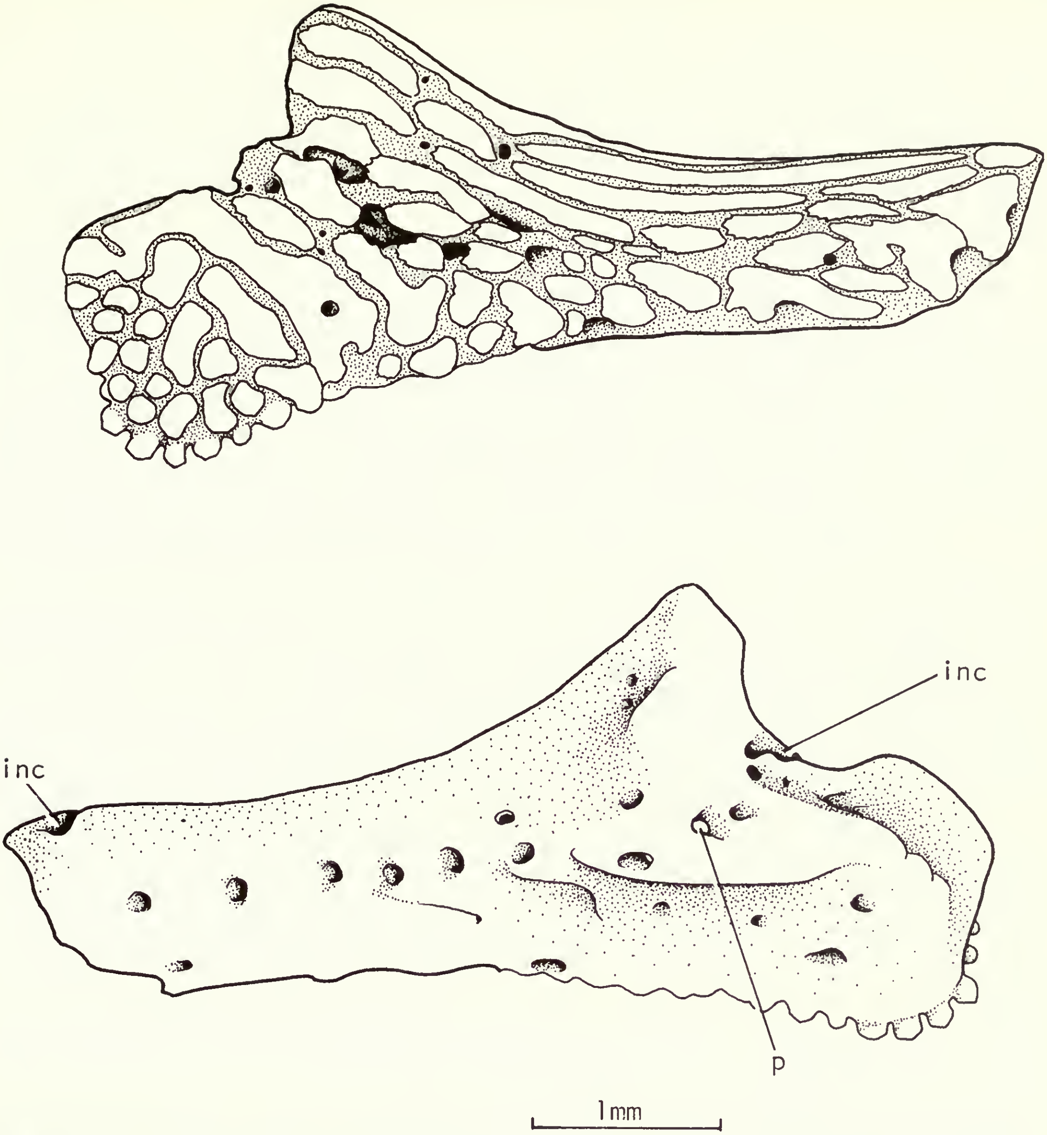

Fig. 74 *Moythomasia durgaringa* Gardiner & Bartram. Left lachrymal in lateral (above) and medial views, from BMNH P.53221.

both an otic process and a prespiracular cartilage are to be found in *Etmopterus* and *Chlamydoselachus*. There is even less evidence to support the view that the lateral commissure is yet another detached otic process, since a lateral commissure also occurs in *Etmopterus*.

5. *Ossifications of the palatoquadrate*. (a) CARTILAGE BONES. In primitive actinopterygians such as *Mimia, Moythomasia, Polypterus* (Allis 1922: 244), *Pteronisculus* (Nielsen 1942: 143) and *Acropholis* (Aldinger 1937: 43) the palatoquadrate ossifies from three centres, the autopalatine, metapterygoid and quadrate. Conditions are similar in more advanced forms such as *Amia, Pholidophorus* and teleosts (e.g. *Salmo, Gasterosteus, Cyclopterus*, de Beer 1937). However, in *Lepisosteus, Macromesodon* (Nursall 1966) and some teleosts there is no autopalatine (Patterson 1973: 246). In larger specimens of *Mimia, Moythomasia, Pteronisculus*, other

palaeoniscids (*Elonichthys, Boreolepis*, Aldinger 1937: 126) and *Ospia* (Stensiö 1932*b*: 252) fusion of individual bones during ontogeny must have occurred because the palatoquadrate is ossified throughout as one bone. In other specimens of *Pteronisculus* (Nielsen 1942: 143), *Saurichthys* (Stensiö 1925: 97), *Acropholis* (Aldinger 1937: 43) and *Boreosomus* (Stensiö 1921: 211) there are only two ossifications. Actinistians have the same three ossifications as actinopterygians (*Nesides*, Jarvik 1954: fig. 15; *Macropoma, Undina, Rhabdoderma*, Forey 1981: fig. 4; *Latimeria*, Millot & Anthony 1958) and this is undoubtedly the primitive osteichthyan condition.

In all described porolepids (Jarvik 1972: 72) and in *Eusthenopteron* (Jarvik 1954: fig. 16) the palatoquadrate shows no signs of subdivision, but is a single ossification, as in larger specimens of *Mimia* and *Pteronisculus*. In *Megalichthys* Watson (1926: 247; fig. 33) described a continuous series of endochondral suprapterygoid bones, but as in his descriptions of palaeoniscid palates Watson (1925: 852; 1928: 52) misinterpreted the material. In his figured specimen of *Megalichthys* the epipterygoid, suprapterygoids and quadrate are all one ossification. In the palaeoniscids *Elonichthys pectinatus* (Watson 1925: 852; fig. 21), *Elonichthys binneyi* (Watson 1925: fig. 22) and *Elonichthys aitkeni* (Watson 1925: fig. 23) the so-called suprapterygoids are all dermal bones (see under dermometapterygoid, p. 310), but in *Nematoptychius greenocki* (Watson 1925: fig. 26; 1928) and *Gonatodus* (Watson 1925: fig. 27) the anterior suprapterygoid is part of the autopalatine and the posterior suprapterygoid is part of the dermometapterygoid. Thus there is no evidence of more than three ossifications in the palatoquadrate of osteichthyans.

The palatoquadrate in Dipnoi is attached to the auditory capsule and to the orbitotemporal region of the neurocranium by the otic and antorbital processes (Sewertzoff 1902: 593), and in Recent forms its only ossification is the quadrate in *Neoceratodus*.

The palatoquadrate in fossil dipnoans is large, rigidly fused to the neurocranium, and ossified throughout as one bone. From its size and complexity in *Dipnorhynchus* (Thomson & Campbell 1971: fig. 27), *Griphognathus, Holodipterus, Chirodipterus* (Miles 1977: figs 14, 22, 35, 53) and *Stomiahykus* (Bernacsek 1977: fig. 8) it is difficult to believe that it is ossified entirely by the quadrate and it is likely that at least a metapterygoid was also present in its ontogeny.

In urodeles and apodans (*Triton, Cryptobranchus, Ichthyophis*) only the quadrate ossifies in the palatoquadrate, as in *Neoceratodus*. But in fossil amphibians such as *Palaeoherpeton* there is both a quadrate and a metapterygoid (the epipterygoid of Watson, 1926). Similarly in lacertilians, chelonians and *Sphenodon* both quadrate and metapterygoid (epipterygoid) are present.

In *Acanthodes* (Miles 1965: fig. 1) three perichondral ossifications exist in the palatoquadrate cartilage, a large quadrate, smaller metapterygoid and much smaller autopalatine. The quadrate and metapterygoid are separated by a large unossified portion, much as in smaller specimens of *Pteronisculus* (Nielsen 1942: 143).

In arthrodiran placoderms the palatoquadrate sometimes contains two perichondral ossifications, an anterior autopalatine and a posterior quadrate which is fused to the inner surface of the postsuborbital (Miles 1971*b*: figs 8, 9B). The two ossifications are separated by a large unossified area as in *Acanthodes* and some specimens of *Pteronisculus*. In *Dicksonosteus* (Goujet 1975: fig. 2) the palatoquadrate is perichondrally ossified as one bone, as it is in *Jagorina* (Stensiö 1969). In the ptyctodont *Ctenurella* (Ørvig 1960, 1962) the palatoquadrate is perichondrally ossified in three separate ossifications, autopalatine, metapterygoid and quadrate, which are of approximately the same size (Miles & Young 1977: fig. 23).

Three ossifications in the palatoquadrate cartilage must be the primitive osteichthyan condition, considered synapomorphous for a group containing acanthodians, placoderms and osteichthyans.

(b) DERMAL BONES. Lining the roof of the mouth of osteichthyans is an extensive sheet of tooth-bearing dermal bones associated with the oral face of the palatoquadrate. In actinopterygians these bones form two series: an outer or ventral arcade comprising the ectopterygoid and dermopalatines and an inner or dorsal series which primitively included dermometapterygoids and an entopterygoid (Fig. 75A, B). In all other osteichthyans the inner or dorsal series (dermometapterygoids and entopterygoid) is absent (Figs 75C, D, 76).

As Rosen *et al.* (1981) suggest, cladistic relationships of sarcopterygians require reduction rather than increase in palatal bones. Thus the presence of demometapterygoid and entopterygoid bones is regarded as primitive rather than a synapomorphy of actinopterygians.

(c) ECTOPTERYGOID. Embryologically the ectopterygoid forms in sequence with the dermopalatines in *Polypterus* (Pehrson 1947: fig. 28), *Amia* (Pehrson 1922) and many teleosts (*Salmo, Clupea*, etc.). In juvenile specimens of *Mimia* (Figs 53, 54), *Pteronisculus, Boreosomus* (Nielsen 1942: figs 34, 71), *Birgeria* (Nielsen 1949: fig. 71) and *Elonichthys* (Watson 1925: fig. 21), the ectopterygoid and dermopalatine clearly belong to the same series.

Primitively the ectopterygoid covers the posteroventral part of the oral face of the palatoquadrate and overlies that part of the palatoquadrate which bounds the adductor opening (*Pteronisculus, Boreosomus, Birgeria, Elonichthys, Mimia, Polypterus*). It also joins the maxilla anteroventrally and the quadrate posteriorly (*Mimia*, Fig. 56; *Pteronisculus, Boreosomus*, Nielsen 1942: 151; fig. 71; *Australosomus, Birgeria*, Nielsen 1949: figs 26, 71; *Elonichthys*, Watson 1925: fig. 22; *Polypterus*, Allis 1922: fig. 25). Further, the centre of ossification of the ectopterygoid is on a level with the most anterior part of the adductor opening, just where the ectopterygoid meets the maxilla (*Pteronisculus*, Nielsen 1942: fig. 37; *Australosomus, Birgeria*, Nielsen 1949: 105, 232; *Mimia*, Fig. 53; *Polypterus*, Pehrson 1947: fig. 28).

Since the ectopterygoid of actinopterygians reaches back to the quadrate and is the posterior member of a series with the dermopalatines, it is clear that this bone is not homologous with the bone called the ectopterygoid in actinistians (*Macropoma*, Watson 1921: fig. 4, ecpt), porolepids (*Glyptolepis*, Jarvik 1972: fig. 31, Ecpt), osteolepids (*Eusthenopteron*, Jarvik 1954: fig. 16, Ecpt) and tetrapods (Presley & Steel 1978: fig. 2, ect). The ectopterygoid of non-actinopterygians compares more favourably with the actinopterygian dermopalatine (see below). On positional and other anatomical and developmental evidence the actinopterygian ectopterygoid is better homologized with the entopterygoid of actinistians, lungfishes and the pterygoid of tetrapods (Figs 75, 76).

(d) DERMOPALATINES. The dermopalatines form a series of interdigitating bones associated with the anteroventral region of the palatoquadrate. Within the palaeoniscids a varying number of dermopalatines has been recorded: four in *Watsonichthys* (Watson 1925: fig. 21, pal.1–4), three or four in *Mimia* (Figs 53, 54), three in *Mesonichthys* (Watson 1925: fig. 23), two in *Elonichthys* (Watson 1925: fig. 22), *Nematoptychius* (Watson 1925: fig. 26), *Pteronisculus, Boreosomus* and *Birgeria* (Nielsen 1942: figs 34, 71; 1949: fig. 71). There is one in *Gonatodus* (Watson 1925: fig. 27), *Namaichthys* (Gardiner 1962: fig. 3) and *Polypterus*. In *Amia* there are two dermopalatines, but in most higher actinopterygians there is only one (*Lepidotes*, Gardiner 1960: fig. 47; *Lepisosteus; Ospia; Elops*, Nybelin 1968: fig. 1). In many teleosts (e.g. *Salmo*, de Beer 1937: 126) this single dermopalatine fuses with the autopalatine to form a composite bone. Dermopalatines are missing in *Australosomus* (Nielsen 1949: fig. 30) and pycnodonts (*Macromesodon*, Nursall 1966). In actinistians the so-called ectopterygoid (Millot & Anthony 1958) is undoubtedly a member of the dermopalatine series; in many fossil forms the corresponding bone is indistinguishable in size and shape from the preceding dermopalatine with which it is closely sutured (e.g. *Macropoma*, P. L. Forey, personal communication). Thus the ectopterygoid of actinistians is better regarded as a posterior dermopalatine, in which case all actinistians possess three dermopalatines as in *Mimia* and *Watsonichthys*.

In porolepids (*Glyptolepis*, Jarvik 1972: fig. 31) the ectopterygoid is again in sequence with an anterior dermopalatine which it resembles in shape, size and disposition of teeth; and similarly in the osteolepids *Eusthenopteron* (Jarvik 1954: fig. 16) and *Glyptopoma* (Jarvik 1950: fig. 6).

Thus in porolepids, osteolepids and onychodonts (Andrews 1973: 146) there are always two dermopalatines (not three as in actinistians), and in this respect these fishes resemble *Amia* and tetrapods. Primitively in tetrapods there are two palatines, an anterior dermopalatine and a more posterior transpalatine (ectopterygoid of Presley & Steel 1978) and their homology with the two dermopalatines in porolepids and osteolepids can be established by positional evidence.

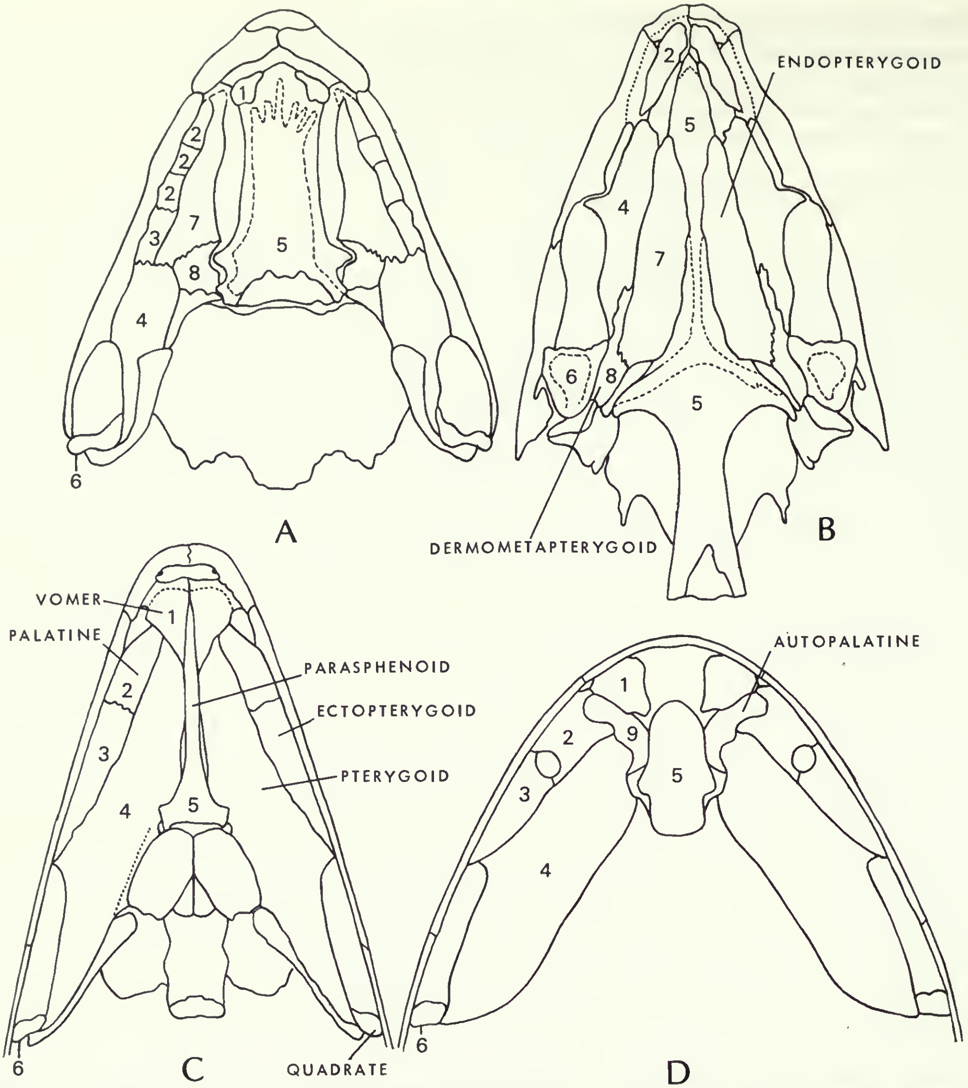
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Fig. 75 Palates in ventral view and suggested homology of dermal bones and their relation to palatoquadrate. A, *Mimia toombsi* Gardiner & Bartram; B, *Polypterus bichir* Saint-Hilaire; C, *Eusthenopteron foordi* Whiteaves (from Jarvik 1954); D, *Glyptolepis groenlandica* Jarvik (from Jarvik 1972). Compare Fig. 76. From Rosen *et al.* (1981).

In Recent dipnoans both dermopalatine and ectopterygoid are missing but in the fossil *Griphognathus* (Miles 1977: fig. 57, Dpl$_2$) one bone of this series remains, which from its position bordering the medial edge of the fenestra ex ochoanalis, must be homologous with the dermopalatine of tetrapods. A similar parallel loss of the transpalatine has occurred in the Lissamphibia; in the urodeles *Salamandra* and *Cryptobranchus* the palatine also disappears at metamorphosis (Wintrebert 1922: 239). The transpalatine is also missing in chelonians and several fossil 'reptiles' (*Placodus, Ichthyosaurus*, etc).

(c) ENTOPTERYGOID. The entopterygoid is a single ossification[1] which occurs in almost all

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[1] Re-examination of the specimen of *Cheirolepis* (BMNH P.36061) described by Pearson & Westoll (1979: fig. 8) has convinced me that what they call lines of individual entopterygoids are no more than fragments of a broken dermal cheek bone.

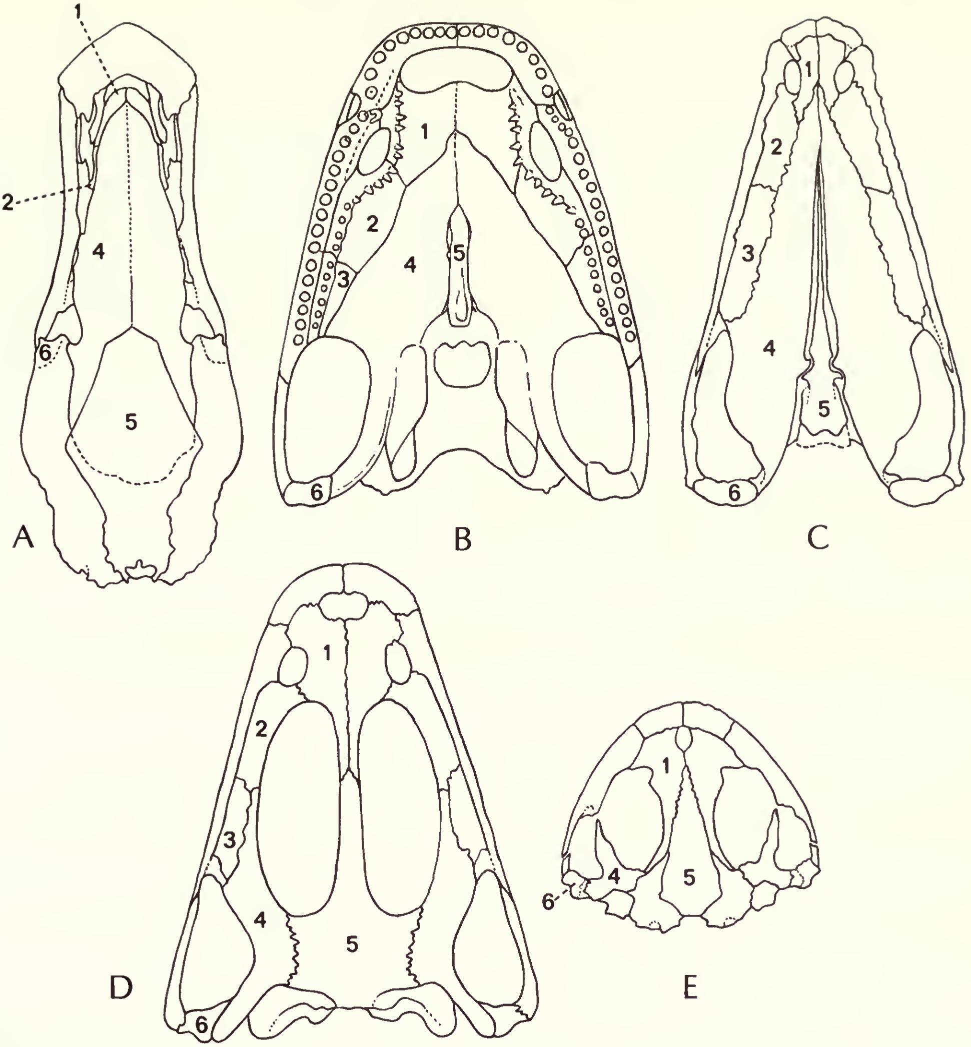

Fig. 76 Palates in ventral view and suggested homology of dermal bones and their relation to palatoquadrate. A, *Griphognathus whitei* Miles (from Miles 1977); B, *Ichthyostega* sp. (from Romer 1966); C, *Eogyrinus attheyi* Watson (from Panchen 1972); D, *Benthosuchus sushkini* Efremov (from Bystrov & Efremov 1940); E, *Tylototriton verrucosus* Riese (from Noble 1931). Compare Fig. 75. From Rosen *et al.* (1981).

actinopterygians with the exception of pycnodonts (*Macromesodon*, Nursall 1966). It is not found in any other osteichthyan. In *Polypterus* the entopterygoid arises in series with the dermometapterygoid (Pehrson 1947: 448), somewhat later in ontogeny than the ectopterygoid and dermopalatine. Although in *Mimia* (Enpt, Figs 53, 54) the entopterygoid could be regarded as being in series with either the ectopterygoid or dermometapterygoids, in most palaeoniscids (and *Polypterus*) it is clearly in series with the dermometapterygoid. Further, in *Pteronisculus* (Nielsen 1942: fig. 37) and *Polypterus* the centres of ossification of the entopterygoid and dermometapterygoid lie near the middle of the dorsal margin of those bones whereas the centres of ossification of the ectopterygoid and dermopalatines are at or near their ventral margins. The centre of ossification of the entopterygoid in *Mimia* also lies near its dorsal margin and similarly in *Amia* and *Elops*.

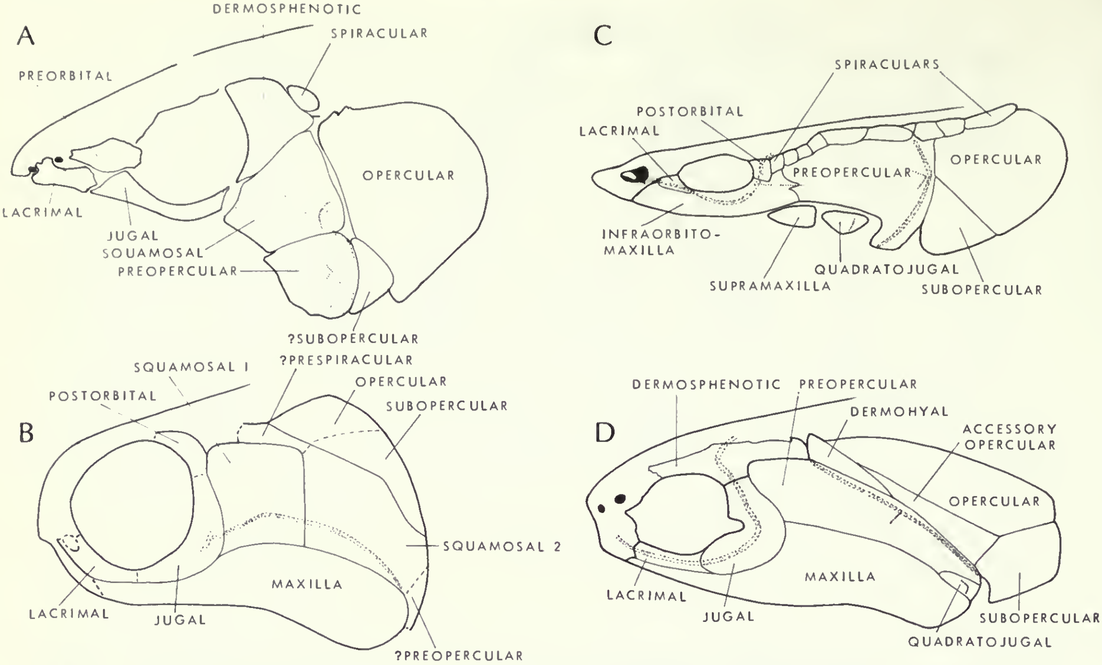
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Fig. 77 Cheek bones and operculum. A, *Rhabdoderma elegans* (Newberry) (after Forey 1981); B, *Strunius walteri* Jessen (after Jessen 1966); C, *Polypterus bichir* Saint-Hilaire (after Daget 1950); D, *Cheirolepis trailli* Agassiz (after Pearson & Westoll 1979). Bone names are those used by the authors cited. From Rosen *et al.* (1981).

The entopterygoid is primitively excluded from the jaw margin by the ectopterygoid and dermopalatines, but in *Australosomus* (Nielsen 1949: fig. 30), where the dermopalatines are absent, the entopterygoid contacts the maxilla anteriorly.

(f) Dermometapterygoid. The dermometapterygoids form a series of interdigitating bones associated with the posterodorsal region of the palatoquadrate, in particular the metapterygoid. *Polypterus* and *Amia* are the only living fish with a dermometapterygoid. Within the palaeoniscids a varying number of dermometapterygoids have been recorded. There are five dermometapterygoids in *Watsonichthys* (Watson 1925: fig. 21, spt) and *Elonichthys binneyi* (Watson 1925: fig. 22, spt 2–6), four in *Mimia* (Dmpt, Figs 53, 54) and *Elonichthys aitkeni* (Watson 1925: fig. 23, the four small bones behind the accessory vomer, spt 1), and one in *Elonichthys caudalis, Elonichthys semistriatus, Gonatodus, Nematoptychius* (Watson 1925: figs 24, 25, 27, metpt; 1928: fig. 7), *Pteronisculus* (Nielsen 1942: fig. 37), *Birgeria* (Nielsen 1949: fig. 71), *Polypterus* and *Amia*. Both entopterygoid and dermometapterygoid bones are primitively present in actinopterygians but neither occurs in other osteichthyans.

We may also conclude that the primitive osteichthyan possessed a further row of tooth-bearing dermal bones consisting of a pterygoid (= ectopterygoid) and several dermopalatines (at least two).

Dermal bones of the cheek: summary and discussion

The bones of the cheek are fairly uniform throughout the osteichthyans (Figs 77, 78). Perhaps the one exception is the osteichthyan dermosphenotic (= postorbital of tetrapods). The dermosphenotic carries the infraorbital canal; it is lateral to the intertemporal in primitive actinopterygians and ventral to the so-called 'dermosphenotic' (Jarvik 1954, 1972) in osteolepids, and is in sequence with the infraorbital bones (jugal and lachrymal). It also forms the dorsolateral border to the spiracle in *Mimia, Moythomasia* and the spiracular pouch in

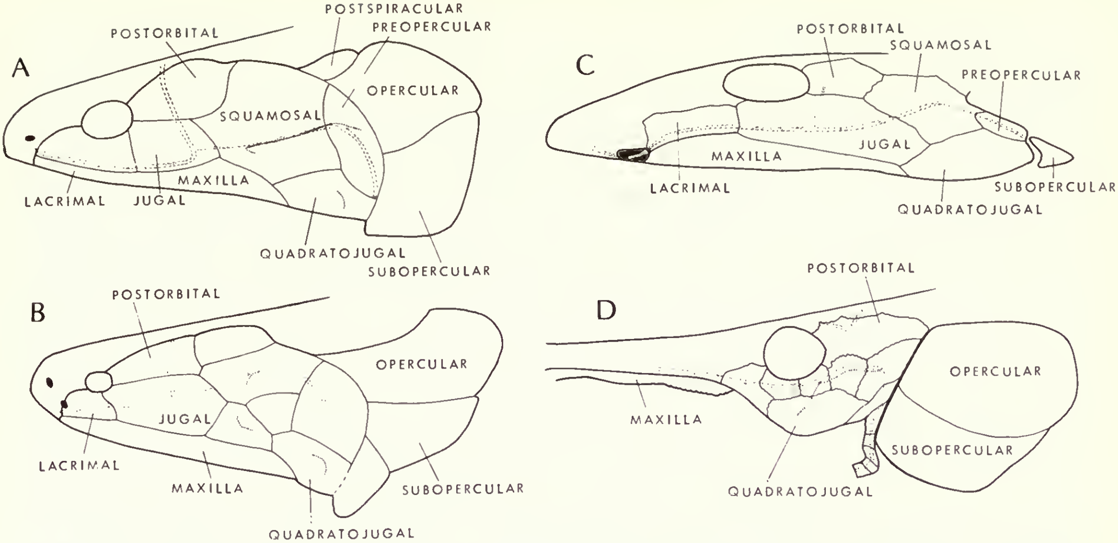
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Fig. 78 Cheek bones and operculum. A, *Eusthenopteron foordi* Whiteaves (after Jarvik 1944*a*); B, *Porolepis brevis* Jarvik (after Jarvik 1972); C, *Ichthyostega* sp. (after Jarvik 1952); D, *Griphognathus whitei* Miles (after Miles 1977). From Rosen *et al.* (1981).

Latimeria; in *Polypterus* and *Acipenser* it lies anterior to the spiracle. It is in contact with the frontals in primitive actinopterygians (*Moythomasia, Mimia, Cheirolepis, Polypterus*) and porolepids (*Holoptychius, Porolepis, Glyptolepis*, Jarvik 1972: figs 43, 44, 45); with the 'dermosphenotic' /X and intertemporal /Y_1 in osteolepids (*Eusthenopteron, Osteolepis*, Jarvik 1972: fig. 61), onychodonts (*Onychodus*) and primitive dipnoans (*Uranolophus, Griphognathus, Chirodipterus,* Miles 1977: fig. 111); with the parietals in actinistians and with the parietals and supratemporals in *Ichthyostega.* In other primitive tetrapods (loxommatids, temnospondyls) it contacts the postfrontal and supratemporal.

Most workers, however, have failed to recognize that the actinopterygian dermosphenotic is homologous with the tetrapod postorbital, because they have been too concerned in trying to find a one-to-one relationship between the cheek and roofing bones of osteolepids and tetrapods. In primitive actinopterygians (*Cheirolepis, Mimia, Pteronisculus*; Fig. 88) there are two bones along the otic portion of the temporal sensory canal (supratemporal and intertemporal). There is one in actinistians and porolepids (supratemporal), but in *Powichthys, Youngolepis*, osteolepids, onychodonts and dipnoans there are three (supratemporal, intertemporal, and 'dermosphenotic'; Jarvik 1972: fig. 61; Miles 1977: fig. 111, Y_2, Y_1, X). Thus, those authors who have accepted Westoll's (1938) theory that the rhipidistian (osteolepid) frontal is homologous with the tetrapod parietal (see p. 320) consider the osteolepid supratemporal to the homologous with the tetrapod tabular, the intertemporal with the supratemporal, and the 'dermosphenotic' with the tetrapod intertemporal (Panchen 1964: fig. 18; Andrews 1973: fig. 3; Vorobjeva 1977*a*: fig. 2). They are then able to homologize the osteolepid postorbital with the tetrapod postorbital and so achieve a one-to-one relationship. Säve-Söderbergh (1932: fig. 15), on the other hand, considered that in *Ichthyostega* the dermosphenotic had fused with the postorbital, but that in other amphibians (*Palaeoherpeton*, Säve-Söderbergh 1935: fig. 41; *Aphaneramma*, Säve-Söderbergh 1936: fig. 31A–D) it has fused with the supraorbital. Stensiö (1947: 93; fig. 26) maintained that in the majority of fossil amphibians, including *Palaeoherpeton*, the dermosphenotic had fused with the postorbital and possibly 'one or a couple of adjoining dermopterotic elements too'. Jarvik (1967*b*: figs 10, 13) supported Säve-Söderbergh as far as *Palaeoherpeton* was concerned, considering the dermosphenotic to have fused with the supraorbital in this form and in 'reptiles', but in temnospondyls he believed it had fused with the intertemporal.

Westoll's (1938) theory concludes that in osteolepids (Fig. 88F) the most anterior element on the main lateral-line (temporal) canal, before the latter turns down onto the cheek (dermosphenotic of Jarvik), is the homologue of the tetrapod intertemporal. Since the intertemporal in tetrapods never has a groove or sulcus for the main lateral-line canal (see for example *Eogyrinus*, Watson 1940: fig. 12), but instead is associated with the supraorbital canal (*Dendrerpeton*, Steen 1934; *Edops*, Romer & Witter 1942; *Trimerorhachis*, Romer 1947: 247; *Palaeoherpeton*, Panchen 1964: 221; fig. 11), it is difficult to homologize the tetrapod intertemporal with the osteolepid 'dermosphenotic'. Similarly, since the main lateral-line canal always passes through the intertemporal in actinopterygians and osteolepids (*Moythomasia*, Jessen 1968: fig. 1, Dsph; *Eusthenopteron, Osteolepis*, Jarvik 1955: fig. 4), where this bone is present, the actinopterygian and osteolepid intertemporal cannot be homologous with the tetrapod intertemporal. This confusion stems from the failure of most authors to recognize that the three bones on the otic portion of the temporal canal of osteolepids are not matched by the three bones in tetrapods. In tetrapods only the supratemporal is associated with the otic portion of the temporal canal. The tetrapod intertemporal, where present, is associated with the supraorbital canal and the tabular with the supratemporal commissure (see below under dermal bones of skull roof, p. 320). In dipnoans there is an additional series of bones between the temporal series and the parietal and median postparietal.

I can now turn to the fusion theory of Säve-Söderbergh (1932: fig. 15; 1935: fig. 41), Stensiö (1947: 93), and Jarvik (1967*b*: figs 10, 13). As pointed out by Jardine (1970: 345), Nelson (1969*a*) and Miles (1977: 221), the terms loss and fusion have no clear meaning when applied to phylogeny so that it is not possible to choose objectively between loss and fusion hypotheses. However, there is no need to infer either in this situation because the homologue of the actinopterygian dermosphenotic is clearly recognizable in tetrapods. Many fossil amphibians have been described in which the temporal canal leaves a well-marked lateral groove on the supratemporal before running onto the postorbital, where it then turns down onto the jugal (*Lyrocephalus, Metoposaurus, Aphaneramma*, Säve-Söderbergh 1937: figs 4A, 12, 31, etc.; *Trimerorachis*, Case 1935). Thus the tetrapod postorbital is the homologue of the actinopterygian dermosphenotic.

The dermosphenotic/postorbital is loosely attached or hinged to the skull roof in many actinopterygians (*Mimia, Stegotrachelus, Lepisosteus*, teleosts), *Gyroptychius* (BMNH 50104), osteolepids, actinistians and porolepids, and this is presumed to be the primitive osteichthyan condition.

The 'dermosphenotic' of *Eusthenopteron* (Jarvik 1972: fig. 61) and *Onychodus* is not homologous with the actinopterygian dermosphenotic; instead it is considered topographically homologous with the 'dermosphenotic' (Fig. 89C) or bone X of dipnoans (Miles 1977: fig. 111).

The remaining cheek bones are less contentious. The jugal canal joins the infraorbital canal below the eye on the suborbital portion of the cheek in actinisitians, onychodonts, porolepids, osteolepids, dipnoans and tetrapods as it does in some selachians and acanthodians. In actinopterygians the jugal canal is wanting except in *Polyodon* and there is usually a single ossification on the preopercular canal, the preopercular. Exceptions include *Boreosomus, Bobasatrania* and *Luganoia* with two ossifications, and *Polyodon* and *Macromesodon* with up to eight tubular bones.

In actinistians, osteolepids and the tetrapods *Ichthyostega* and *Acanthostega* (Säve-Söderbergh 1932: fig. 15; Jarvik 1952: fig. 33a), there are normally two bones on the preopercular–jugal canal, whereas in porolepids (Jarvik 1972: figs 43, 44) there may be three, in dipnoans six (*Neoceratodus*) or seven (*Griphognathus*, Miles 1977: fig. 112), and in tetrapods other than *Ichthyostega* and *Acanthostega* one, the squamosal. By comparing *Ichthyostega* and *Acanthostega* with other osteichthyans, the squamosal is presumed to be homologous in actinistians, tetrapods and osteolepids and the condition in dipnoans, where there are numerous elements, is derived. The actinopterygian condition, with the preopercular extending forwards above the posterior expansion of the maxilla, is likewise derived.

In primitive actinopterygians (*Cheirolepis, Mimia, Moythomasia*), osteolepids (*Eusthenopteron, Osteolepis, Eusthenodon*) and some tetrapods (*Ichthyostega, Acanthostega, Palaeoher-*

peton) the lower margin of the cheek is formed by the quadratojugal and the toothed maxilla. Porolepids and *Polypterus* are similar except that here the preopercular also contributes to the lower margin. In actinistians the quadratojugal is wanting and possibly the maxilla also, and in this latter respect actinistians parallel later dipnoans. Thus a separate quadratojugal (bone 10) is still recognizable in many early dipnoans such as *Dipnorhynchus* (Thomson & Campbell 1971: fig. 7), *Griphognathus* and *Chirodipterus* (Miles 1977: figs 112, 117, bone 10), where it is associated with the cheek pit-line as in actinopterygians, osteolepids, porolepids and some tetrapods (*Palaeoherpeton*, Panchen 1964: fig. 12). Furthermore the bone described as an ectopterygoid in *Griphognathus* by Miles (1977: fig. 57), and which bites outside the lower jaw, is most probably a maxilla (Rosen *et al.* 1981: fig. 7).

The remaining bones of the cheek constitute the infraorbital series which together form the hind and lower borders of the orbit. In primitive actinopterygians (*Mimia, Moythomasia*) and in actinistians (*Macropoma, Rhabdoderma, Latimeria*), osteolepids and porolepids there are only two bones in this series, as in all tetrapods. It seems likely therefore that they are homologous with the jugal and lachrymal. In later actinopterygians the number of bones in the infraorbital series is greatly increased and may be as high as seven in many teleosts (Nelson 1969*a*: 4). In osteolepids and porolepids the condition is often obscured by ontogenetic fusion of the bones anteriorly. Nevertheless in most described cases at least two bones are recognizable, the jugal and lachrymal of Jarvik (1980). In *Panderichthys* (Vorobjeva 1977*b*: fig. 2), however, there are as many as four elements. In dipnoans the number of infraorbitals is more variable and in this respect they parallel later actinopterygians. Thus there are four infraorbitals in *Neoceratodus*, five in *Dipnorhynchus, Scaumenacia, Griphognathus* and *Sagenodus*, and six in *Chirodipterus* and *Dipterus*.

A summary of the dermal bone homologies outlined above is presented in Table 1, p. 323.

Sensory canals of the cheek: summary and discussion

The preopercular canal joins the infraorbital canal behind the orbit and beneath the spiracle in actinistians, porolepids, osteolepids, onychodonts, dipnoans and amphibians. The preopercular canal also joins the infraorbital canal ventral to the spiracle in *Polyodon* but in this instance (as in *Macromesodon*) the cheek plates are reduced and the canal runs in a series of tubular ossicles, a condition which is assumed to be secondary (Stensiö 1947). This connection between the preopercular and infraorbital sensory canals is generally referred to as the jugal line or canal (hyomandibular line; angular–jugal line; supramaxillary line) since in sharks it often differentiates as an independent line (Rudd 1920). In sharks the jugal line is invariably connected to the infraorbital canal from which it may also develop (Holmgren 1940: 85). Usually the jugal canal is not joined posteriorly to the preopercular canal but in some specimens of *Chlamydoselachus* and in *Torpedo* it links the infraorbital and preopercular canals (Holmgren 1942: fig. 19). The jugal canal also grows out from the postorbital portion of the infraorbital canal in *Neoceratodus* (Allis 1934: 369), but in amphibians (Platt 1896, Stone 1922) this connection is achieved by a branch of the preopercular canal growing forwards and downwards across the cheek to meet the infraorbital canal. The preopercular canal is also joined to the infraorbital canal by the jugal canal in many acanthodians and placoderms and this is presumed to be the primitive gnathostome condition.

In actinopterygians, where there is no connection between the two canals, there is a horizontal pit-line in the position of the jugal canal which is similarly innervated by a branch of the mandibular nerve (hyoideo-mandibularis of Pehrson 1947). This pit-line is not found in other groups and it is also missing in *Polyodon*; it is generally considered to be the homologue of the jugal canal of other forms (Stensiö 1947). The horizontal pit-line arises from the upper part of the preopercular canal in *Polypterus* and *Amia* (Allis 1889: Pehrson 1947) and remains intimately connected with it in both embryo and adult. Traces of the anterior limits of the horizontal pit-line are found on the maxilla of *Polypterus* (Jarvik 1947: fig. 1A) and *Moythomasia*.

A further pit-line is present in many osteichthyans, the vertical pit-line (or postmaxillary line, Stensiö 1947). This line is usually in two parts and the dorsal component meets the horizontal

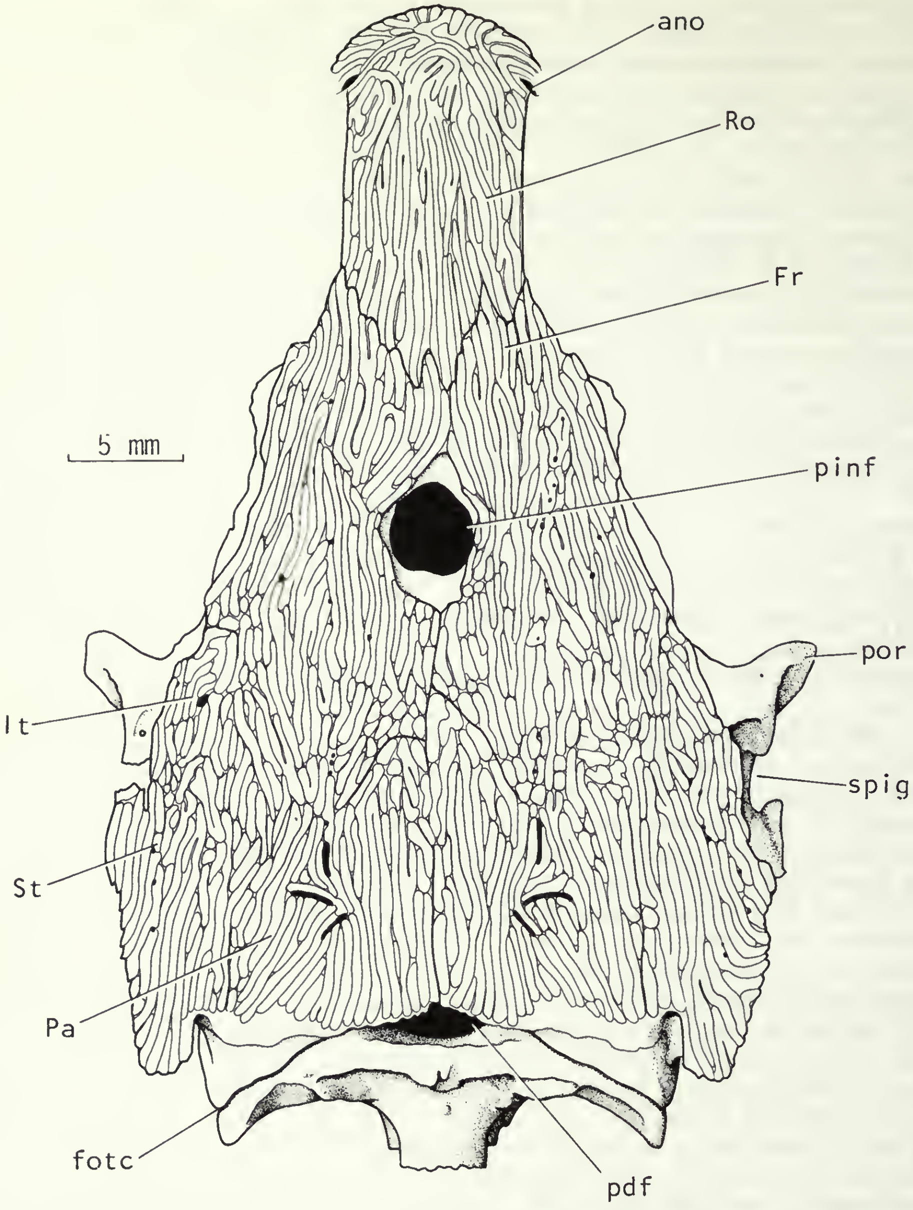


Fig. 79 *Mimia toombsi* Gardiner & Bartram. Neurocranium and attached dermal bones in dorsal view, from BMNH P.53243.

pit-line to give a >-shaped structure in primitive actinopterygians (*Mimia, Polypterus*). The ventral part of this line in actinopterygians crosses the quadratojugal when this bone lies near the surface (*Mimia, Polypterus, Pteronisculus*). In more advanced actinopterygians (*Lepisosteus, Amia*) the vertical pit-line is in one piece. The vertical pit-line is also in two parts in some actinistians (*Rhabdoderma*), porolepids (*Holoptychius*), osteolepids (*Eusthenopteron*), some dipnoans (*Dipterus*) and a few primitive amphibians (*Palaeoherpeton*), with the ventral portion crossing the quadratojugal where this bone is present. The line is single in *Griphognathus, Neoceratodus* and *Protopterus*. The vertical pit-line meets or crosses the jugal canal in sharks (*Chlamydoselachus*), actinistians (*Nesides, Rhabdoderma*), osteolepids (*Eusthenopteron*) and

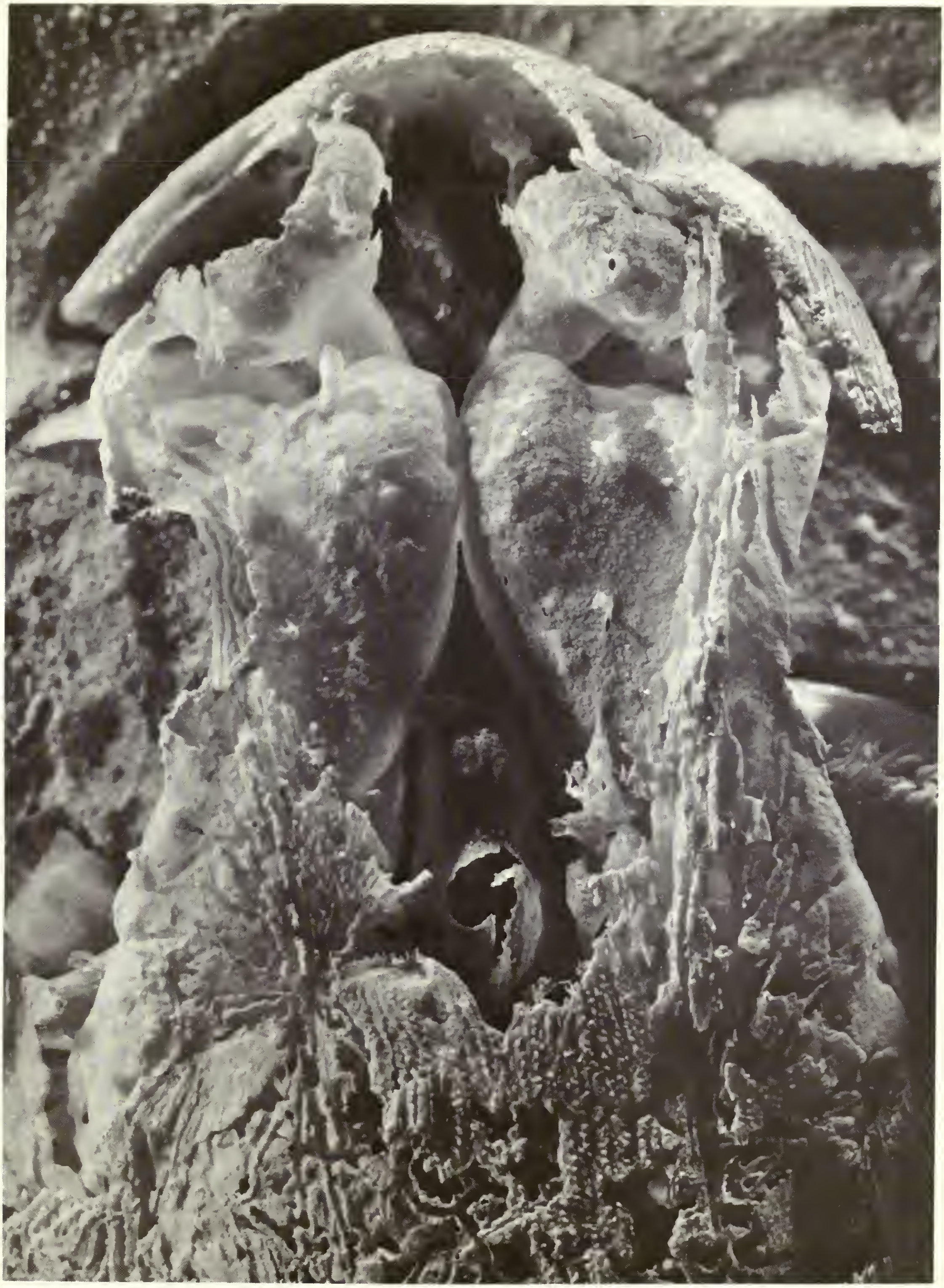


Plate 1 *Mimia toombsi* Gardiner & Bartram. Braincase in dorsal view, from P.56505, ×11½.

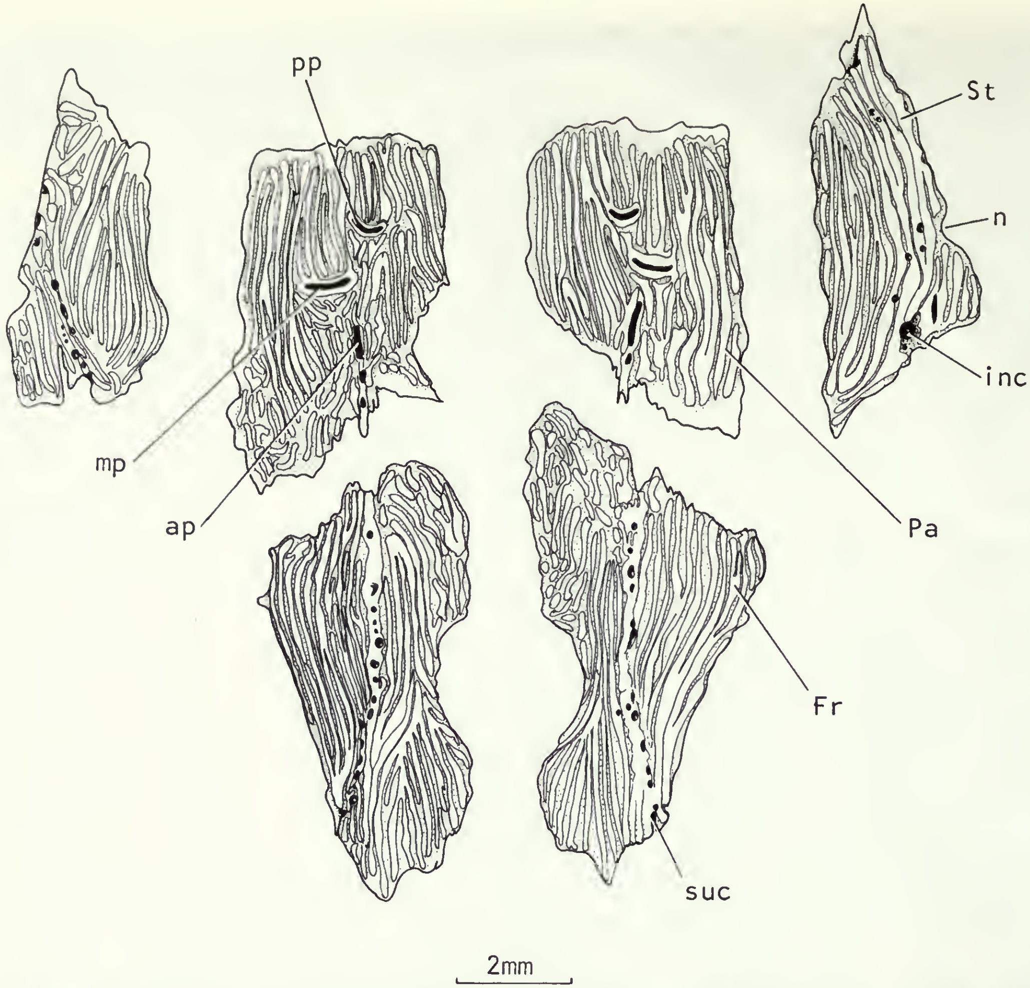


Fig. 80 *Mimia toombsi* Gardiner & Bartram. Dermal bones of the skull roof in dorsal view (intertemporal missing), from BMNH P.56473.

dipnoans (*Griphognathus, Protopterus*). The absence of a squamosal bone and a jugal sensory canal are considered autapomorphous for actinopterygians.

Dermal bones of the skull roof

Mimia toombsi

The dermal bones on the dorsal surface of the neurocranium anterior to the occipital fissure are closely applied to the dorsal neurocranial surface. Even the nasals may have a fragile attachment at points where the delicate perichondral nerve canals join the underside of the supraorbital sensory canal (Pl. 1). The only areas where this attachment is less than secure is where the perichondral lining of the neurocranial roof is interrupted posteriorly around the lateral cranial canal and anteriorly in front of the pineal foramen.

The parietal is roughly rectangular in outline, somewhat longer than broad and with its radiation centre beneath the middle pit-line. It has a zigzag suture anteriorly with the frontal. Ventrally two sets of nerve foramina presumably served for branches of the glossopharyngeal nerve (fb.IX, Fig. 81) to the middle pit-line and for branches of the vagus (fb.X, Fig. 81) to the

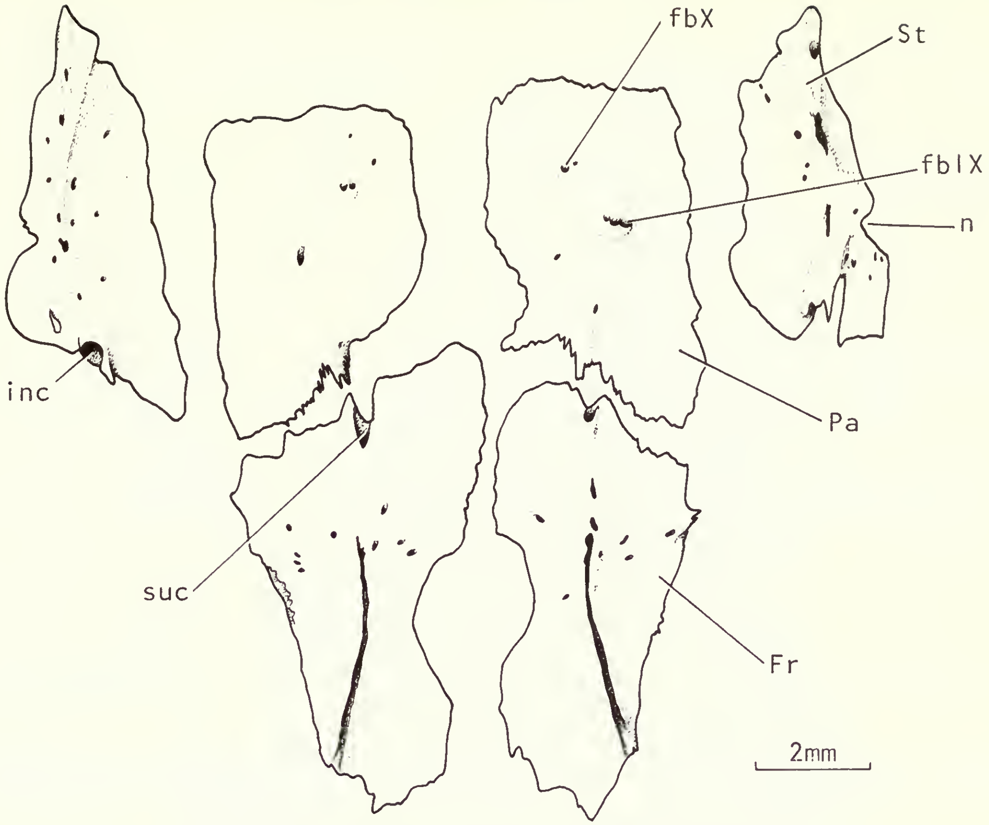


Fig. 81 *Mimia toombsi* Gardiner & Bartram. Dermal bones of the skull roof in ventral view (intertemporal missing), from BMNH P.56473.

posterior pit-line. The anterior pit-line is continuous with the supraorbital canal which leaves the parietal through a tongue-shaped projection of the anterior margin.

The largest element of the dermal roof is the paired frontal which tapers to a point anteriorly. Posteriorly it forms a slight overlap with the parietal. The radiation centre is nearer the posterior than anterior margin, at the level of the rear of the pineal foramen. The supraorbital canal pierces the radiation centre. The anteromedial margin of the frontal has a zigzag suture with the rostral while the anterolateral corner sutures with the nasal. Ventrally the passage of the supraorbital sensory canal is marked by a rounded ridge which may have a slit-like opening anteroventrally (Fig. 81).

The supratemporal is a long, narrow bone which is sutured medially to the parietal and anteriorly to the intertemporal. There is a small notch in its lateral margin (n, Figs 80, 81) dorsal to the head of the hyomandibula. This notch, present in the lateral margin of the intertemporal of many actinopterygians (*Cheirolepis, Pteronisculus, Elonichthys, Moythomasia*), was said by Aldinger (1937: 249) to be related to the underlying fossa bridgei and by Jessen (1968: fig. 1) to be the spiracular opening. But there is no fossa bridgei in *Mimia* or *Moythomasia* and the spiracular opening is between the intertemporal, supratemporal and dermosphenotic. Instead I postulate that this notch allowed the head of the hyomandibula greater flexibility in respiratory movements. The supratemporal is traversed by the otic part of the main lateral-line canal which passes through the radiation centre. This centre lies just behind the notch in the lateral margin. Anterolaterally a flange of the supratemporal forms the posterolateral margin of the spiracular opening (Fig. 82).

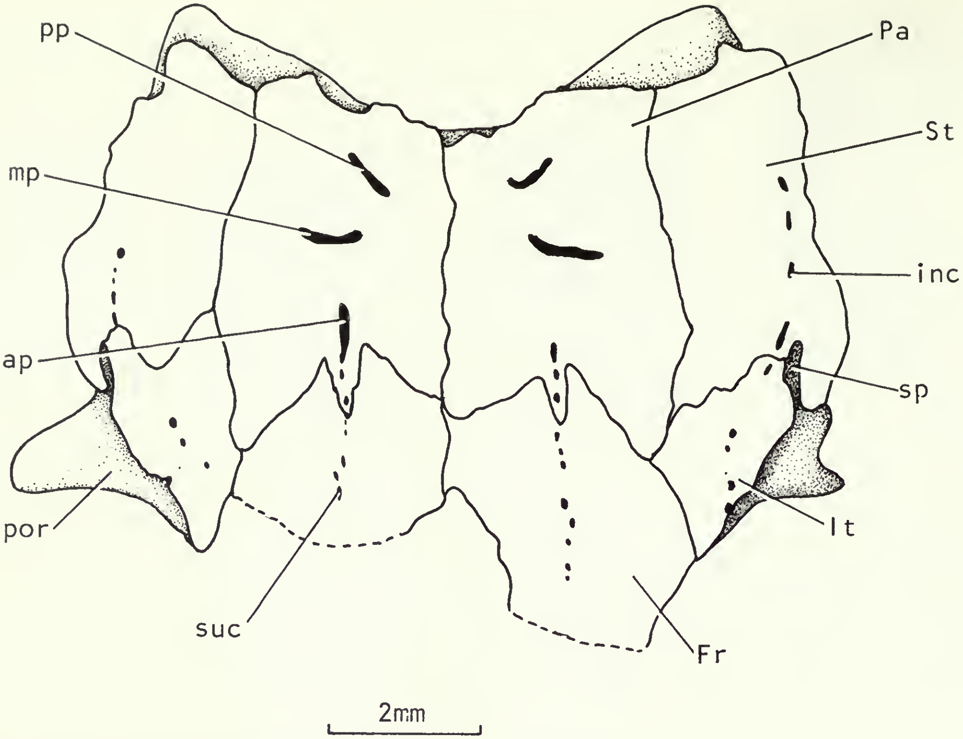


Fig. 82 *Mimia toombsi* Gardiner & Bartram. Otic and orbitotemporal regions of neurocranium and attached roofing bones in dorsal view, from BMNH P.53259.

The intertemporal is a small triangular bone sitting above the postorbital process. It sutures with the parietal and supratemporal posteriorly and with the frontal medially. Its radiation centre is pierced by the main lateral-line canal and lies near the posterior margin. The passage of the sensory canal through both temporal bones is marked ventrally by a rounded ridge.

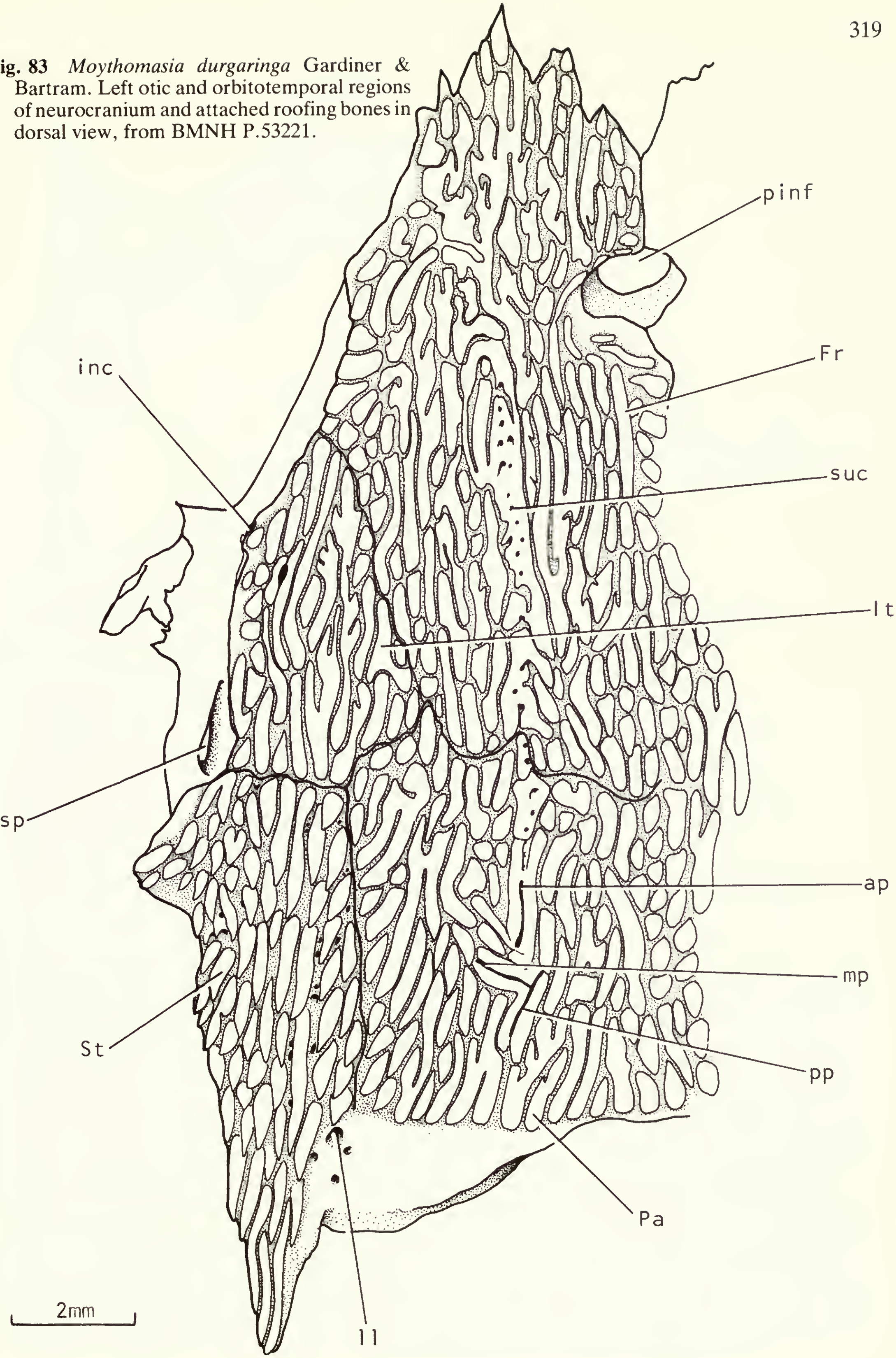
The extrascapular series consist of a single pair of bones which just meet in the midline. Anteriorly the extrascapular sits on the slightly bevelled transverse margin of the parietals. Posteriorly and laterally the extrascapular overlies the occipital region of the neurocranium, covering the posterior dorsal fontanelle and part of the occipital fissure. The supratemporal commissure pierces the bone in a transverse direction and the cephalic division of the main lateral-line runs in a longitudinal direction. The radiation centre is situated at the confluence of these two canals. A posterolateral peg-like projection (Figs 84, 85) of the extrascapular passes under the post-temporal, while its posterior margin rests on an anterior flange of the post-temporal.

Moythomasia durgaringa

The parietals and frontals are very similar to those of *Mimia* (Fig. 83). However, the posteroventral margin of the parietal is more shelf-like than in *Mimia* and more intimately fused with the underlying neurocranium. The posterior corner of the supratemporal is also more markedly pointed. The extrascapular series consists of two pairs of bones, a smaller medial pair and a much larger lateral pair (Fig. 87).

The lateral extrascapular contacts the parietal anteriorly, but laterally sits on an inwardly-directed flange of the supratemporal. The medial extrascapular comprises two components: an anterior plate of bone and a posterior tubular portion for the supratemporal commissure.

Fig. 83 *Moythomasia durgaringa* Gardiner & Bartram. Left otic and orbitotemporal regions of neurocranium and attached roofing bones in dorsal view, from BMNH P.53221.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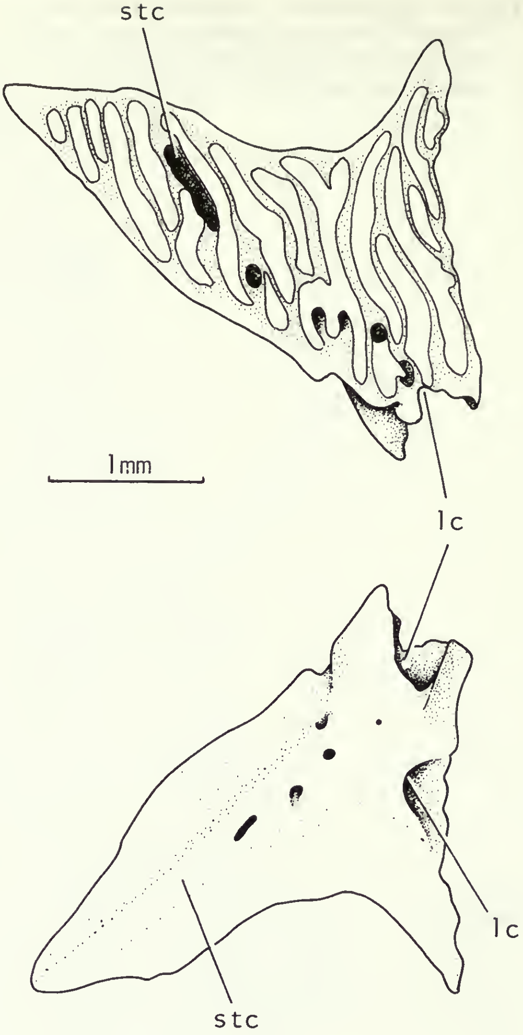

Fig. 84 *Mimia toombsi* Gardiner & Bartram. Right extrascapular in dorsal (above) and ventral views, from BMNH P.54498.

Dermal bones of skull roof: summary and discussion

1. *Homologies of dermal bones of skull roof*

The osteichthyan dermal roofing bones form two distinct patterns (Rosen *et al.* 1981). The more primitive is believed to be that found in actinopterygians, osteolepiforms, porolepiforms and actinistians, in which the paired frontals and parietals form the major constituents of the skull roof and the parietals reach the posterior limits of the otic region of the underlying neurocranium. The pineal foramen is invariably situated between the frontals. The alternative, derived pattern is seen in dipnoans and tetrapods (Fig. 89), where there is a cluster of at least two pairs of bones behind the parietals and the pineal foramen lies either between the parietals or just anterior to them (*Dipnorhynchus*, later tetrapods).

The two pairs of bones covering the dorsal side of the otic region in actinopterygians, osteolepiforms, porolepiforms and actinistians were originally called frontals and parietals because they appeared to be homologous with those bones in mammals. The cluster of six bones behind the parietals in primitive tetrapods were called postparietals, tabulars and supratemporals. Lying behind these skull roofing bones and therefore not attached to the under-

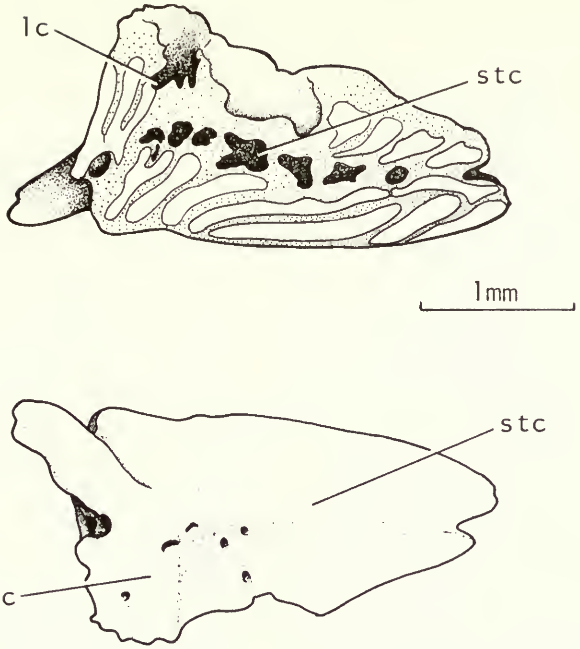

Fig. 85 *Mimia toombsi* Gardiner & Bartram. Left extrascapular in dorsal (above) and ventral views, from BMNH P.56497.

lying neurocranium is a series of scale bones or extrascapulars (Jollie 1981). This series is missing in tetrapods.

In the search for tetrapod origins it was necessary to reconcile these two distinct dermal roofing bone patterns, because osteolepiforms were thought to include the tetrapod ancestor. Thus Säve-Söderbergh (1932) proposed that the ancestral dermal roof of crossopterygians and tetrapods must have contained two pairs of frontals and parietals and that the tetrapod parietal and postparietal should be regarded as fronto-parietal and parieto-extrascapular respectively. The assumption that the extrascapular series of scale bones could in some way become intimately associated with the otic region of the neurocranium had already been proposed by Watson & Day (1916) when they homologized the crossopterygian medial extrascapular with the tetrapod postparietal and the lateral extrascapular with the tabular. This theory, subsequently modified by Säve-Söderburgh (1935, 1936) and championed by Jarvik (1967*b*: 205), demands that a transverse series of scale bones moved forward onto the neurocranium. As Rosen *et al.* (1981: 222) have pointed out, the dermal roofing bones in osteichthyans (and placoderms – see Jarvik 1967*b*: fig. 3) are frequently attached to the underlying neurocranium by descending laminae of membrane bone. Where laminae are missing the dermal bones may be equally tightly attached to the underlying perichondral bone as in *Mimia, Moythomasia* and *Eusthenopteron* (Jarvik 1975: fig. 13). It therefore appears unlikely that these dermal roofing bones would have been able to move forward on the otic region to make room for the extrascapular series. Moreover, in many dipnoans the cluster of five roofing bones (behind the parietals) is followed by a series of extrascapular scale bones which lie loosely behind them (Miles 1977: figs 111, 116, 118), free of the underlying otic region of the neurocranium.

An alternative theory to that of Watson & Day (1916) was Westoll's (1936, 1938) proposition that the crossopterygian frontal was homologous with the tetrapod parietal. Westoll's theory demands the reverse of Watson & Day's: that is, it assumes that there was a backward movement of the parietals, again without regard to the underlying neurocranium. To accept Westoll's theory is to deny the presence of frontals in all bony fishes with the exception of the osteolepids, *Elpistostege* and *Panderichthys* and certain dipnoans (*Dipterus, Uronemus,*

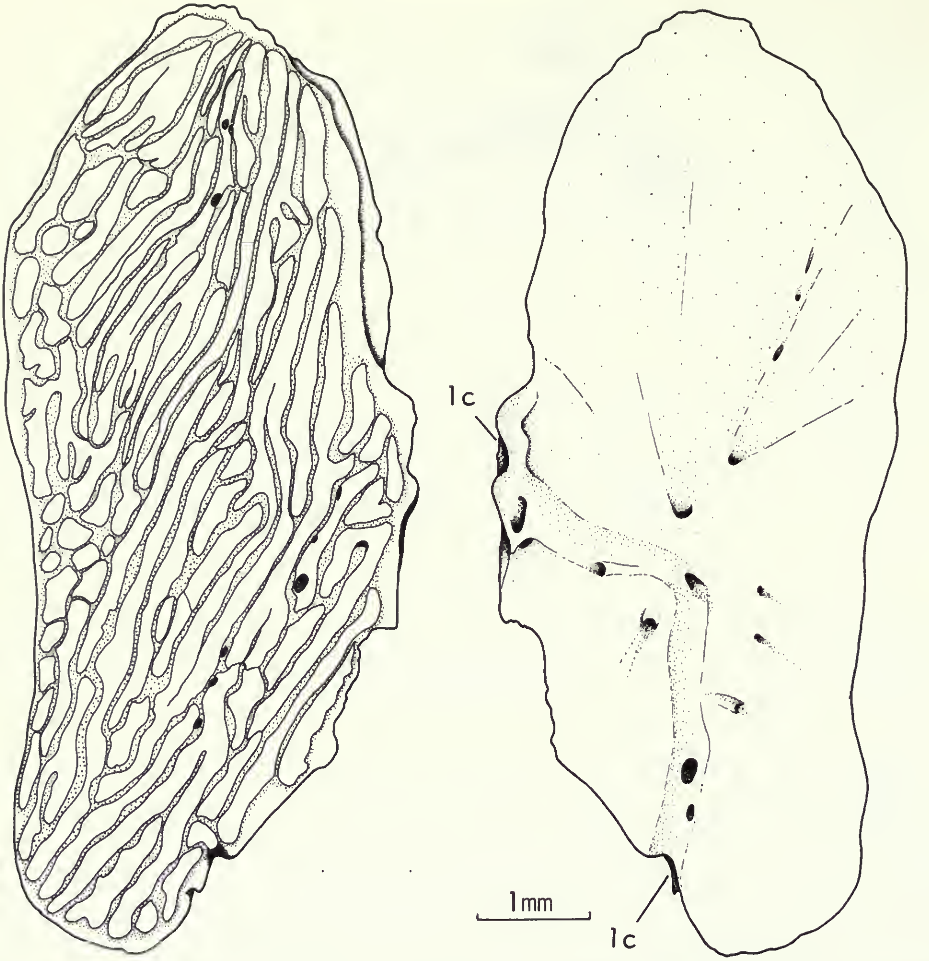

Fig. 86 *Mimia toombsi* Gardiner & Bartram. Right post-temporal in dorsal (left) and ventral views, from BMNH P.56498.

Rhinodipterus, Scaumenacia, Ctenodus). I have suggested (Gardiner 1980) that an extra pair of bones in *Panderichthys* be called postparietals, but they are associated with transverse pit-lines (Vorobjeva 1977*b*: fig. 2B) and are better homologized with the parietals of *Eusthenopteron*.

The temporal bones (intertemporal, supratemporal /Y_1Y_2) have already been discussed (see p. 311), but it is worth noting that in later actinopterygians (e.g. many palaeoniscids, *Lepisosteus, Amia*, teleosts) the two temporal bones are replaced by a single dermopterotic. A single bone similarly occupies this position in *Ichthyostega*, most temnospondyls, and primitive amniotes where it is called the supratemporal. Two temporal bones occur in some loxommatids, a few temnospondyls, anthracosaurs and *Seymouria*.

From the evidence given above it seems that the tetrapod supra- and intertemporal are not homologous with similarly-named bones in other osteichthyans. If this conjecture is correct, then those bones associated with the otic portion of the infraorbital sensory canal in primitive osteichthyans are absent in tetrapods. Support for this suggestion is afforded by living amphibians where the otic part of the infraorbital line is reduced to a single organ (Platt 1896; Stone 1922) and by primitive fossil amphibians where the infraorbital line ends blindly in the postorbital (*Ichthyostega, Loxomma, Crassigyrinus*, etc.).

Table 1 The positional homologies of dermal skull and cheek bones in Osteichthyans.

Primitive Actinopterygians *(Mimia, Moythomasia)*	*Eusthenopteron*	Porolepiformes	Actinistians	Dipnoans	*Ichthyostega*	Primitive Tetrapods
Frontal	Frontal	Frontal	Frontal	Frontal/E Parietal/C	Frontal Parietal	Frontal Parietal
Parietal	Parietal	Parietal	Parietal	Median postparietal/B	Median postparietal	Postparietal
Dermosphenotic	Postorbital	Postorbital	Postorbital	Postorbital/4	Postorbital	Postorbital
Intertemporal	Dermosphenotic			Dermosphenotic		
	Intertemporal			Intertemporal/Y1,X		
Supratemporal	Supratemporal	Supratemporal	Supratemporal	Supratemporal/Y2		
				K		Intertemporal
				Anterior lateral parietal/J	Supratemporal	Supratemporal
				Posterior lateral parietal/I	Tabular	Tabular
Jugal Lachrymal	Jugal Lachrymal	Jugal Lachrymal	Jugal Lachrymal	Infraorbitals/5,6,7,1	Jugal Lachrymal	Jugal Lachrymal
Preopercular	Squamosal Preopercular	Squamosal Preopercular Preoperculo-submandibular	Squamosal Preopercular	8+9a–f	Squamosal Preopercular	Squamosal
Quadratojugal	Quadratojugal	Quadratojugal		10	Quadratojugal	Quadratojugal
Maxilla	Maxilla	Maxilla		Maxilla	Maxilla	Maxilla
Premaxilla	Premaxilla	Premaxilla fused into snout	Premaxilla	Premaxilla fused into snout	Premaxilla	Premaxilla
Nasal	3 Nasals	4–5 Nasals	3 Nasals	4–10 Nasals	Nasal	Nasal
2–4 Extrascapulars	3 Extrascapulars	3 Extrascapulars	3–7 Extrascapulars	3 Extrascapulars		

Behind the parietals and postparietal of actinopterygians, actinistians, rhipidistians and dipnoans lie the transverse series of extrascapular bones. In actinopterygians this series frequently consists of a single pair of bones (e.g. *Cheirolepis, Mimia, Amia, Elops*). In other actinopterygians it comprises two pairs of bones (*Polypterus, Moythomasia, Lepisosteus*), but in *Acipenser* it is made up of a lateral pair with a much larger median element. A pattern similar to that of *Acipenser* is found in most osteolepids, porolepids, onychodonts and primitive actinistians (*Diplocercides, Rhabdoderma*). In later actinistians the number of lateral extrascapulars increases; thus in *Diplurus* there are three lateral pairs and in *Latimeria* there are four pairs as well as the median element. The condition in dipnoans is less clear, although there appears to be a median element and at least one pair of lateral bones in primitive forms (*Griphognathus, Chirodipterus, Dipterus, Scaumenacia*, Jarvik 1968; Miles 1977). An additional pair of scale bones which are not canal-bearing occurs in *Griphognathus* and *Chirodipterus*, whereas in *Dipnorhynchus* there are three pairs of canal-bearing lateral bones and a median element (Thomson & Campbell 1971). Outside the osteichthyans a single pair of scale-like extrascapulars (or postnuchals) has been recorded in a few advanced placoderms such as the coccosteids *Millerosteus* and *Dicksonosteus*, and a median extrascapular is said to be present in the actinolepid *Sigaspis* (Goujet 1973). In the coccosteids the extrascapulars are traversed by the supratemporal commissure. Although the placoderms show a third pattern of dermal roofing bones, little of this pattern matches either of those seen in osteichthyans. However, the presence of large dermal roofing bones with descending laminae and contained tubular sensory canals in at least the presumed primitive placoderms (Miles & Young 1977) is considered synapomorphous for a group including placoderms and osteichthyans.

2. *Sensory canals of skull roof*

The supraorbital canal joins the infraorbital canal above the eye in most living actinopterygians (*Polypterus, Acipenser, Polyodon, Amia, Lepisosteus*, many teleosts). Nevertheless the two canals arise separately and in *Amia* the supraorbital canal anastomoses with the infraorbital by the penultimate primary pore and then continues back onto the parietal (Allis 1889). The two canals remain separate in many primitive actinopterygians such as *Cheirolepis, Mimia, Moythomasia* and *Elonichthys*, as well as in more advanced forms like caturids, pachycormids and *Leptolepis*.

The canals join behind the eye in actinistians (e.g. *Nesides, Rhabdoderma, Whiteia, Diplurus, Latimeria*) and in all described osteolepiforms (e.g. *Eusthenopteron, Osteolepis*), porolepiforms (e.g. *Holoptychius, Glyptolepis, Porolepis*) and *Powichthys*. In dipnoans the canals are separate in *Uranolophus* and *Dipnorhynchus*, but join behind the eye in almost all other forms (*Griphognathus, Chirodipterus, Dipterus, Fleurantia, Neoceratodus, Protopterus*). Again in many fossil tetrapods (*Trematosaurus, Lyrocephalus, Batrachosuchus*) the canals remain separate, but in others like *Trimerorhachis, Metoposaurus* and in living genera such as *Pelobates* they join behind the orbit. In most selachians (e.g. *Chlamydoselachus, Mustelus, Torpedo*) and holocephalans (e.g. *Callorhynchus, Chimaera*), although the two canals invariably develop independently (Rudd 1920, Holmgren 1940), they join behind the eye in the adult (Garman 1888). In *Laemargus* (*Somniosus*), however, Garman (1888) concluded that the two canals remained separate, but Ewart (1895) showed that the infraorbital and supraorbital canals open to the exterior by a common pore. They agreed that the remaining lines terminated independently on the top of the head in *Laemargus*. In placoderms the infra- and supraorbital canals or lines remain separate in such diverse forms as *Lunaspis, Holopetalichthys, Romundina, Arctolepis* and *Leiosteus*, whereas they may join in a somewhat unusual fashion in *Coccosteus* and *Ctenurella* (Miles & Young 1977). The pattern of the pit-lines on the head of arthrodires and phyllolepids, where three sets of lines converge (supraorbitals, infraorbitals/central canal, posterior pit-lines) is very similar to that in the selachian *Laemargus*. This similarity may be regarded either as a synapomorphy of placoderms and *Laemargus* or as the retention of the primitive gnathostome condition. The presence of three pairs of converging pit-lines on the parietals of actinopterygians (and their innervation, Allis 1922, Pehrson 1947) and on the posterior parietals of many fossil dipnoans (*Griphognathus, Chirodipterus*, Miles

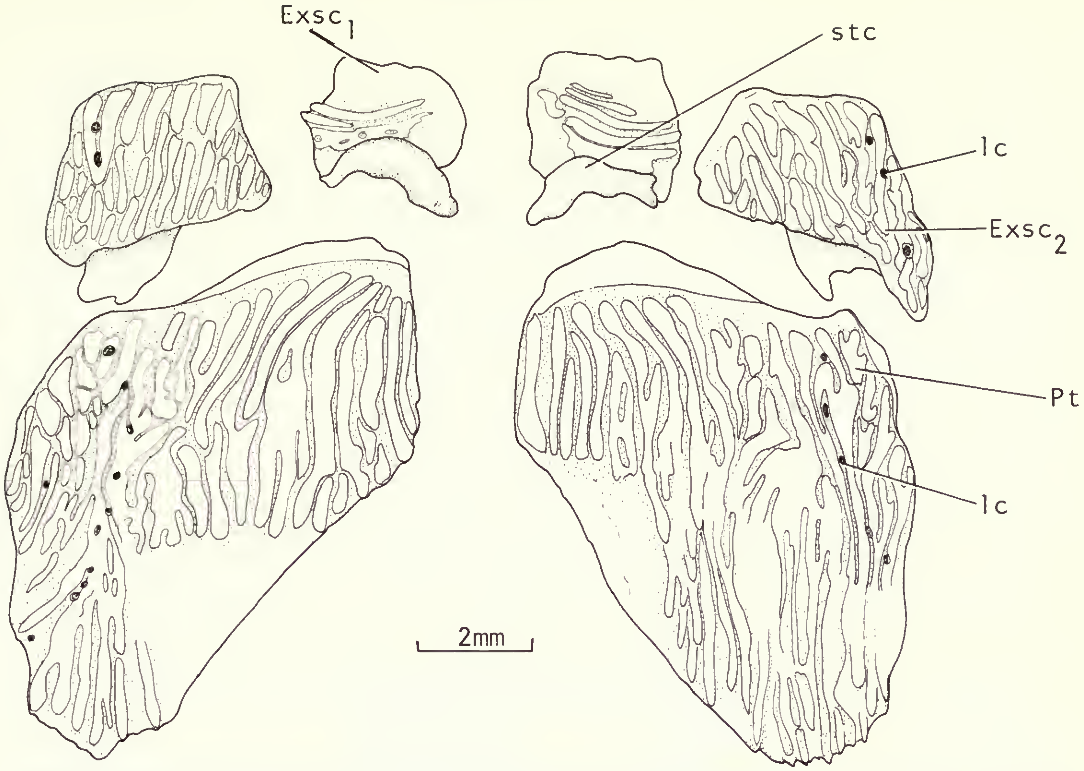

Fig. 87 *Moythomasia durgaringa* Gardiner & Bartram. Extrascapulars and post-temporals in dorsal view, from BMNH P.53221.

1977: figs 113, 116; *Rhinodipterus, Scaumenacia*) convinces me that the latter view is the more likely.

In acanthodians the infra- and supraorbital canals always remain separate (e.g. *Euthacanthus, Ischnacanthus, Diplacanthus, Homalacanthus, Acanthodes*, Watson 1937), and in *Diplacanthus* the infraorbital canal is continued up on the top of the head as the central sensory line. In this respect *Diplacanthus* resembles placoderms and *Laemargus* and this must be the primitive condition. Thus we may conclude that primitively in gnathostomes the infraorbital and supraorbital canals were separate.

Lower jaw

Mimia toombsi

The Meckelian cartilage is ossified throughout its length in presumed older individuals. In less well ossified specimens there are two perichondral ossifications, one anteriorly and one posteriorly. In others the perichondral covering is complete apart from the glenoid fossa and there are endochondral cores anteriorly and posteriorly. These ossifications are the mentomeckelian and articular bones. Separate mentomeckelian and articular bones are only distinguishable in a few specimens (cf. BMNH P.56473) and even so the mentomeckelian usually has the two anterior coronoids closely applied to its medial surface.

Where ossification is complete all the exposed surfaces of the Meckelian bone are perichondrally ossified except in the glenoid fossa. The bulk of the articular region is formed of dense endochondral bone. Posterodorsally the glenoid fossa is represented by two distinct depressions which match the double condyle of the quadrate. Posteriorly and ventrally the

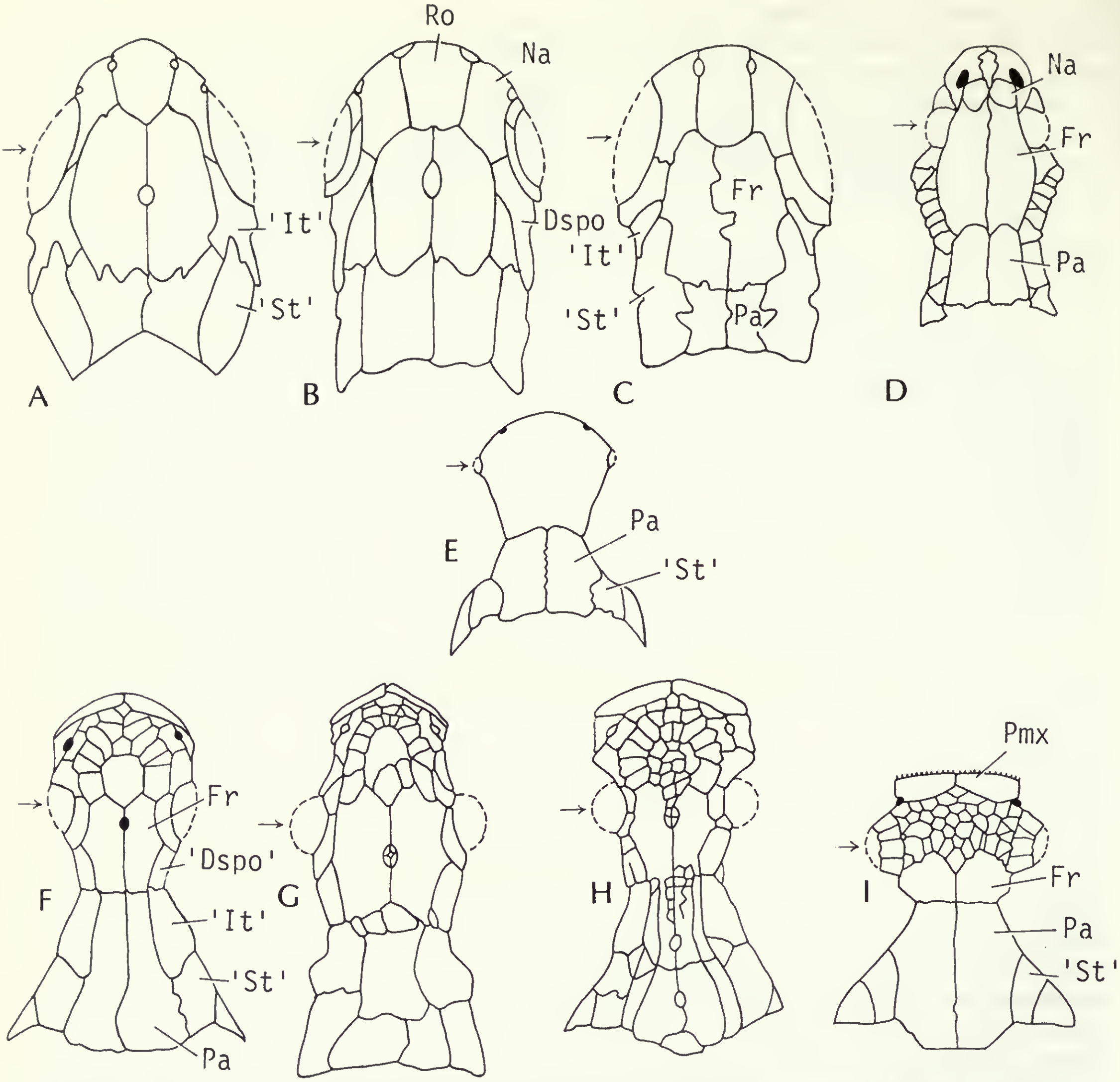

Fig. 88 Skull roofs. A, *Kentuckia deani* (Eastman) (from Rayner 1951); B, *Moythomasia nitida* Gross (from Moy-Thomas & Miles 1971); C, *Pteronisculus magnus* (Nielsen) (from Nielsen 1942); D, *Polypterus* sp. (from Schmalhausen 1968); E, *Porolepis brevis* Jarvik (from Jarvik 1972); F, *Eusthenopteron foordi* Whiteaves (from Jarvik 1967*b*); G, *Eusthenopteron,* composite, showing variations in bone patterns (from Jarvik 1967*b*); H, composite showing maximum number of separate bones observed in *Osteolepis, Thursius,* and *Gyroptychius* (from Jarvik 1948); I, *Holoptychius* sp. (from Jarvik 1972). Scale bones at back of braincase omitted. From Rosen *et al.* (1981).

articular is free of any dermal bone investment, as is the greater part of the ventromedial face of the Meckelian bone.

There is a distinct groove (gmand.ext.VII, Fig. 91) behind the lateral corner of the glenoid fossa. The groove continues anteriorly on the medial surface of the dentary. Several foramina on the dentary open into this groove, and presumably served for the innervation of that section of the mandibular sensory canal. An identical groove has been recorded in *Pteronisculus* (Nielsen 1942: figs 38, 40, sm). By comparison with *Polypterus* (Allis 1922) the groove is presumed to

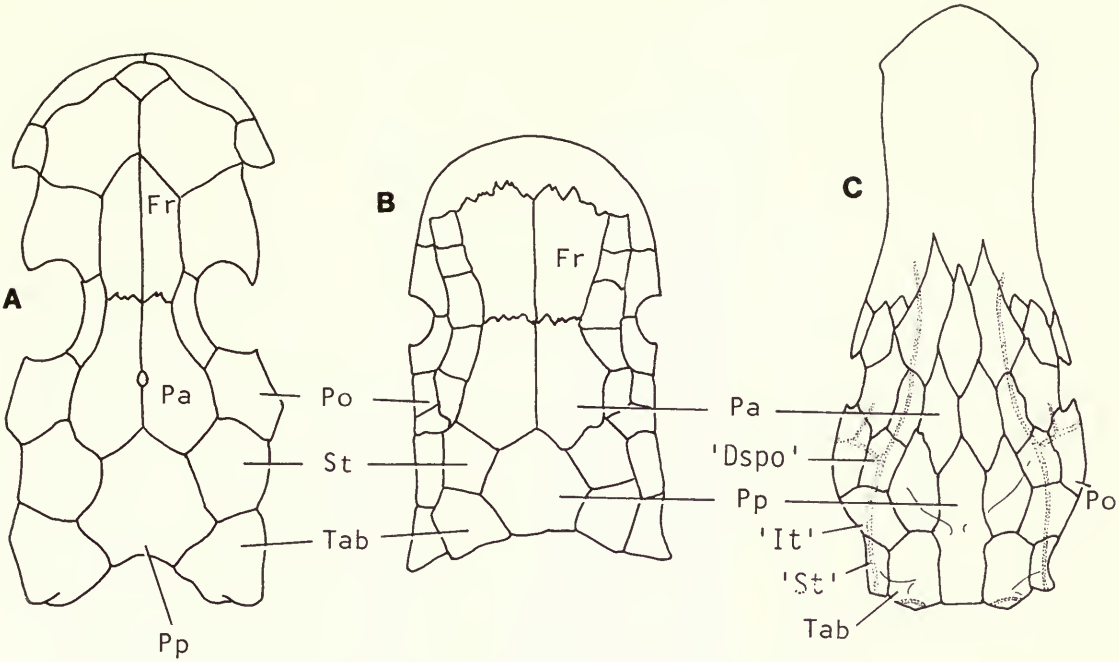

Fig. 89 Skull roofs. A, *Ichthyostega* sp. (from Romer 1966); B, *Scaumenacia* sp.; C, *Griphognathus whitei* Miles (from Miles 1977).

have carried the external mandibular branch of the facial nerve. Three or four large foramina (fmand.V, Fig. 91) in the ventral margin of the Meckelian bone, anterior to the junction of the angular and dentary, presumably served for the passage of branches of the trigeminal nerve from the adductor fossa into this groove, as in *Polypterus*.

On the medial face of the Meckelian bone and a little way in front of the top of the previously mentioned groove is a distinct foramen (fmand.int.VII, Fig. 91). This foramen leads into a canal which passes anterodorsally between the prearticular and the perichondral covering of the Meckelian bone and then between the posterior coronoid and the perichondral covering of the Meckelian bone. The canal finally opens into the groove between the coronoids and the dentigerous edge of the dentary, as in *Polypterus*. The canal therefore must have transmitted the internal mandibular branch of the facial nerve. A similar canal has been described in *Pteronisculus, Birgeria* (Nielsen 1942, 1949) and other palaeoniscids (Poplin 1974: fig. 40).

Anteriorly the Meckelian bone is densely ossified in the region of the mentomeckelian ossification. The mentomeckelian bone extends back beneath the coronoids where it merges indistinguishably with the anterior end of the articular. Beneath the coronoids the mentomeckelian bone is ridged in an anteroposterior direction. This ridging is presumed to represent the area of origin of the geniohyoideus muscle, this being precisely its area of origin in *Polypterus* (Allis 1922: 255). The same ridges may also be for the intermandibular muscles. In the same region of *Pteronisculus* (Nielsen 1942: 165) there is a series of shallow depressions.

The external surface of the mandible is composed of two dermal bones, the dentary and the angular. Together they form the outer boundary of the adductor fossa. The angular forms the hind margin of the mandible and is roughly triangular in outline. The mandibular canal pierces it from end to end, passing through the radiation centre which is marked by a slot-like pit-line. In its posterior margin the angular has a small depression (pchl, Fig. 90). This is presumed to have been the origin of the ceratohyal ligament, as in *Polypterus* (Allis 1922: 246). A similar ligament in *Lepisosteus* (Wiley 1976) has its origin on the retroarticular. Anterodorsally the angular is joined to the dentary by an interdigitating suture. The angular and dentary in this region are

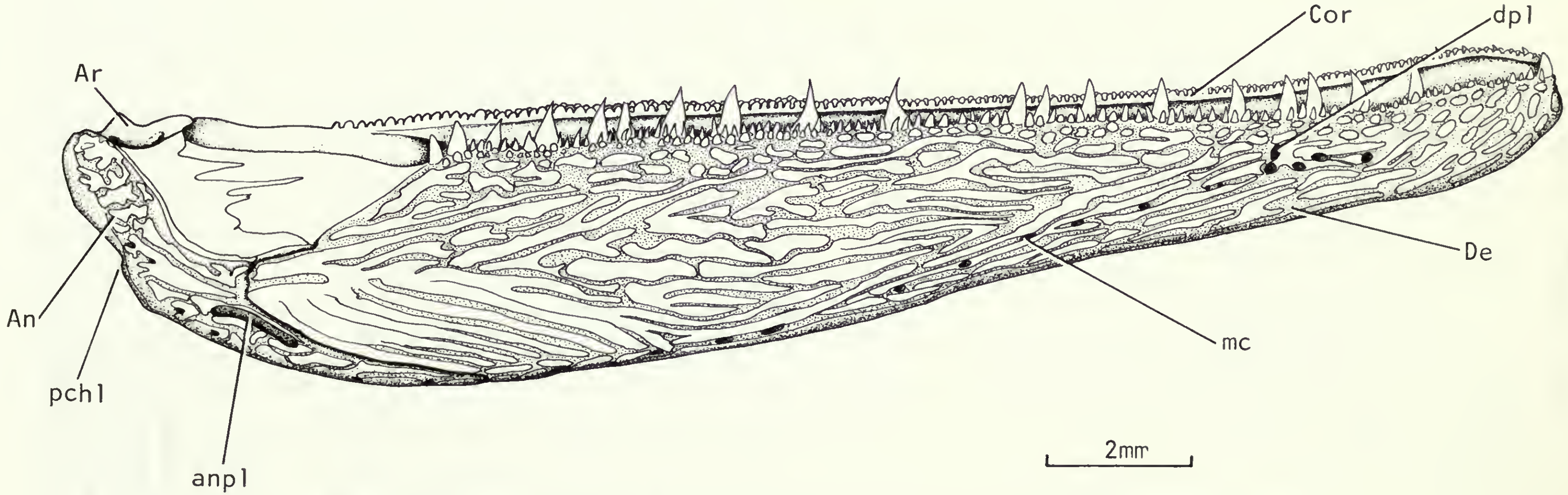
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Fig. 90 *Mimia toombsi* Gardiner & Bartram. Right lower jaw in lateral view, from BMNH P.56498.

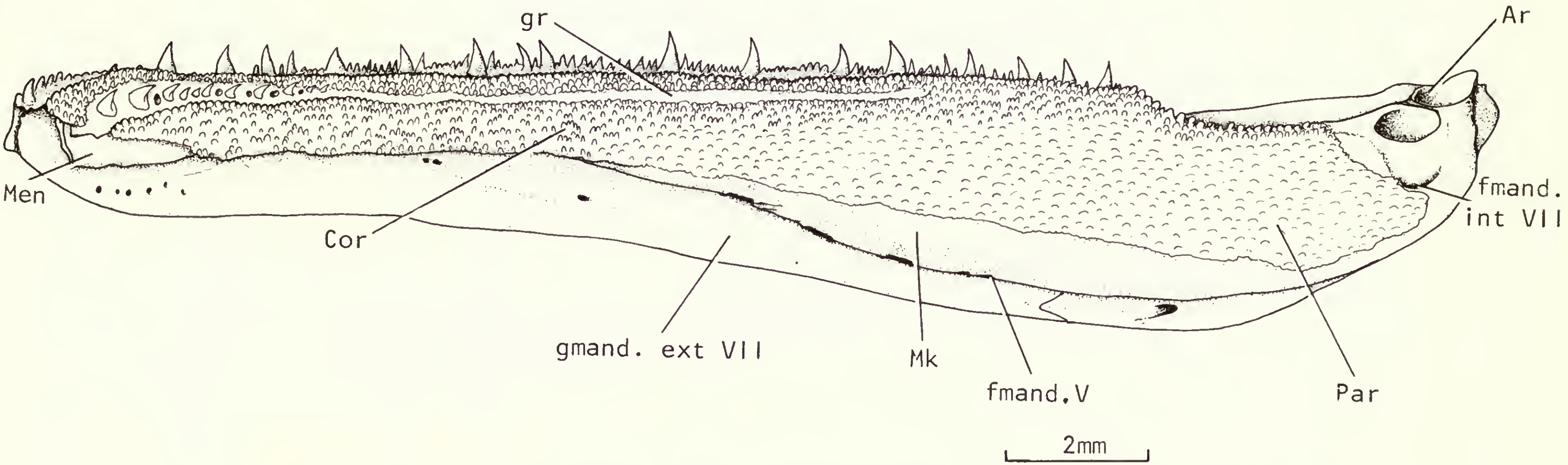
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Fig. 91 *Mimia toombsi* Gardiner & Bartram. Right lower jaw in medial view, from BMNH P.56498.

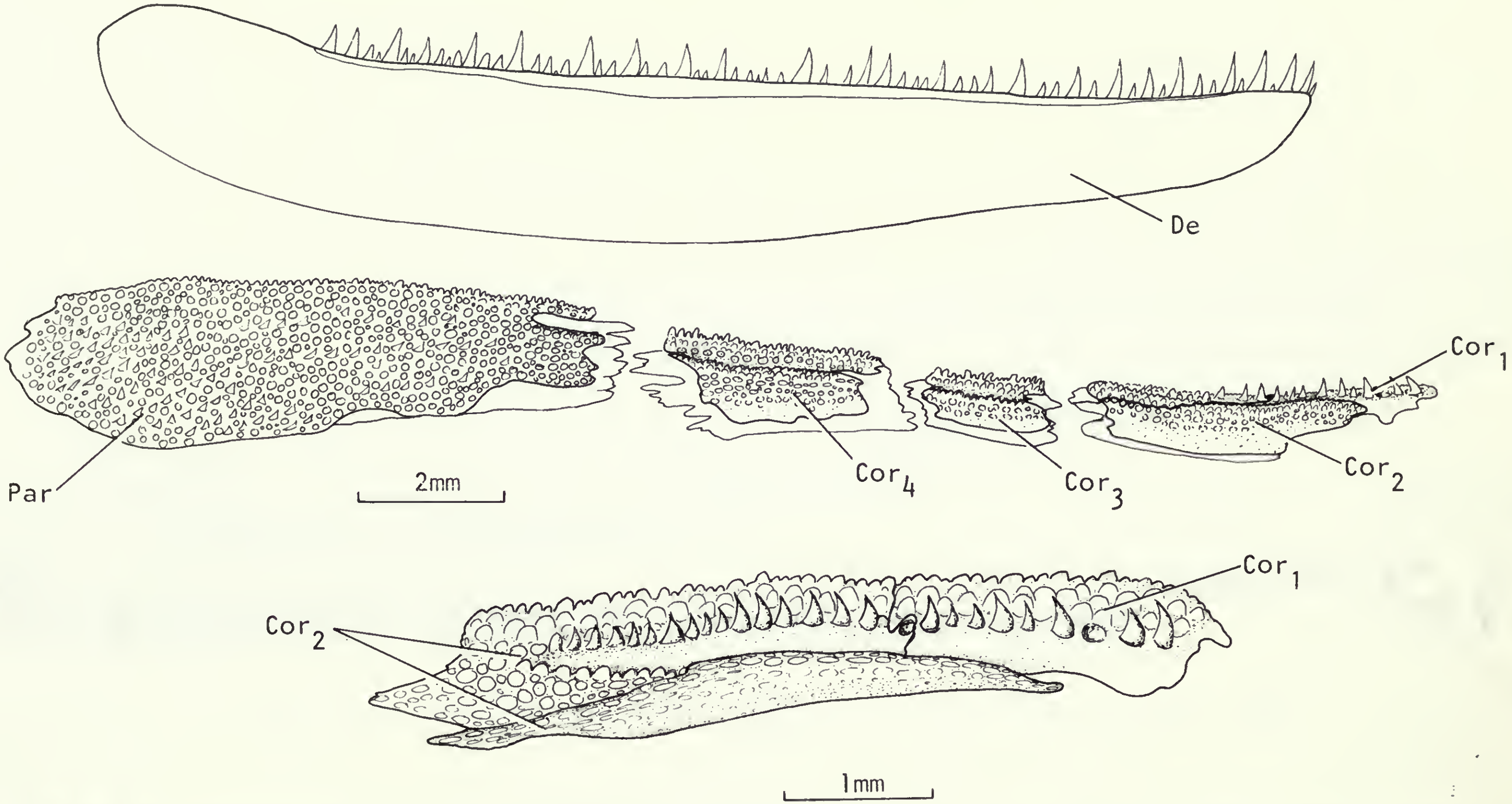
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Fig. 92 *Mimia toombsi* Gardiner & Bartram. (A), left dentary, and associated tooth plates of an incompletely ossified individual, in medial view; (B), anterior coronoids more highly magnified; all from BMNH P.56473.

devoid of ornamentation and the triangular area of smooth bone represents exactly that part of the mandible permanently overlapped by the maxilla. The radiation centre of the angular lies near the posterodorsal corner.

The dentary is very long and its anterior end curves medially. It bears on its dorsal edge a row of sharp, stout teeth, and outside this row there are numerous smaller teeth. The larger teeth possess an apical cap of acrodin (Pl. 4, c). The dentary overlaps the angular posteroventrally and is traversed for almost its full length by the mandibular sensory canal. The canal enters the dentary at its most ventral point of contact with the angular and from there the canal rises at a low angle up through the dentary, changing direction somewhat anteriorly. Where the canal changes direction there is a group of five pores and this represents the radiation centre. Two of these pores form a pit-line and in other specimens a distinct anterodorsal slot is developed in this region. A dentary pit-line has only been recorded elsewhere in *Polypterus* (Jarvik 1947: fig. 1A). An oral sensory canal is found in the surangular of dipnoans.

By far the largest dermal bone on the medial side of the mandible is the prearticular, which covers the dorsal and much of the medial face of the Meckelian bone in the region of the adductor fossa. Posteriorly this bone ends on the lateral face of the Meckelian bone just behind the glenoid fossa. It extends anteriorly for half the total jaw length, much as in *Pteronisculus*. The prearticular is gently rounded dorsoventrally, with its dorsal surface forming a horizontal lamina in front of the adductor fossa. This lamina contacts the horizontal lamina of the dentary laterally, while anteriorly it bears a groove which is continuous with that on the coronoids (gr, Fig. 91). The groove is a mirror image of a similar groove on the dermopalatines. The whole of the outer surface of the prearticular is covered by a shagreen of small rounded teeth similar to those on the palate. The radiation centre lies dorsally, immediately anterior to the adductor fossa. Anteriorly the prearticular is joined to the fourth coronoid by a deeply interlocking zigzag suture. Similar sutures are present between successive coronoids. The coronoid series consists of four bones of which the posterior is the largest. The third and fourth coronoids are of the same general shape with a gently rounded medial lamina and a grooved, stouter horizontal lamina. Their radiation centres lie in the middle of the bones in the anteroposterior groove. They are covered with a similar shagreen of rounded teeth as is found on the prearticular. The two anterior coronoids are invariably closely applied to the underlying mentomeckelian bone and the first coronoid does not possess a medial lamina. Instead the tuberculated lamina of the second coronoid (Fig. 92) is produced anteriorly and overlies the posteromedial surface of the first coronoid. A similarly-situated bone in the anterior part of the mandible of *Pteronisculus* (Nielsen 1942: figs 38, 39, 40, Mmd), said by Nielsen to contain both an endochondral and a dermal component, may be reinterpreted as the medial lamina of a coronoid fused to the underlying mentomeckelian, as in *Mimia*.

The two anterior coronoids have, in addition to their small teeth, a row of larger, acutely pointed teeth along the outside of the aforementioned groove.

Moythomasia durgaringa

The mandible of *Moythomasia* is similar to that of *Mimia* but differs in the presence of a supra-angular.

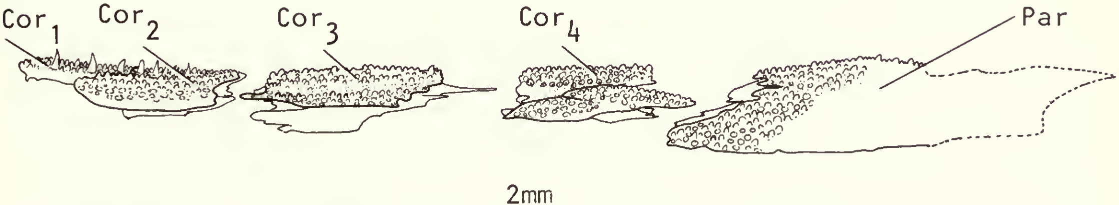


Fig. 93 *Mimia toombsi* Gardiner & Bartram. Dermal tooth plates of the right lower jaw of an incompletely ossified individual in medial view, from BMNH P.56473.

The prearticular consists of two ossifications: there is a separate, much smaller, posterior ossification overlying the entrance to the canal for the internal mandibular branch of the facial nerve. The prearticular teeth are confined to the posterior and dorsal margins of the first prearticular and the medial laminae of the coronoids are mostly toothless. The supra-angular is a stout ossification which forms the lateral border of the adductor fossa. It overlaps the dentary and prearticular anteriorly and the angular ventrally. Posterodorsally it is attached to the articular. All four coronoids bear a row of much larger, acutely pointed teeth. These are continuous with a few similar teeth on the anterior portion of the first prearticular.

Lower jaw: discussion

1. *Meckelian ossifications*

In presumed juveniles of *Mimia* and *Moythomasia* a thin perichondral sheath is present round the anterior and posterior ends of Meckel's cartilage, much as in *Acanthodes* (Miles 1973*a*, Jarvik 1977). Later an endochondral core forms in the articular posteriorly and in the mentomeckelian bone anteriorly. Eventually these two ossifications meet and the whole cartilage is endochondrally and perichondrally ossified. It is then usually referred to as the Meckelian bone. A fully-developed Meckelian bone is characteristic of most adult palaeoniscids, including *Mimia, Moythomasia, Pteronisculus* and *Boreosomus*, of *Australosomus*, of osteolepids such as *Eusthenopteron* and *Panderichthys*, porolepids such as *Glyptolepis*, and primitive dipnoans (*Griphognathus, Chirodipterus, Holodipterus, Melanognathus, Dipterus*). Two discrete ossifications separated by cartilage are characteristic of *Polypterus*, parasemionotids, *Pholidophorus germanicus*, fossil actinistians such as *Rhabdoderma, Diplocercides, Coelacanthus* and *Coccoderma*, and tetrapods such as *Ichthyophis, Cryptobranchus* and *Lacerta*. But in *Lepisosteus*, most teleosts and *Latimeria* the posterior end of Meckel's cartilage possesses two ossifications, the articular proper and the retroarticular, whereas in *Amia* there are three (two articulars and a retroarticular). There are also two posterior ossifications (in tandem) in several fossil actinistians (*Macropoma, Laugia, Whiteia*), but in larger specimens of *Whiteia* and in *Rhabdoderma* there is only a single ossification (P. L. Forey, personal communication). Nelson (1973) concluded that the presence of a discrete articular and retroarticular was a plesiomorphic character of actinopterygians, whereas Patterson & Rosen (1977: 129, character 19) considered an independent retroarticular the derived condition. Yet even if we allow that the articular bone in fossil actinistians is developed from two ossification centres (articular, retroarticular) which may fuse during ontogeny, its single nature in *Polypterus* and Recent amphibians suggests that this is the primitive adult osteichthyan condition.

In placoderms the Meckelian cartilage ossified perichondrally in two regions, as in acanthodians and presumed juvenile *Mimia*. In placoderms and acanthodians the cartilage frequently calcifies, in placoderms invariably as globular calcified cartilage. They are referred to as the mentomandibular and articular ossifications, and are characteristic of many arthrodires (Stensiö 1963*a*, Miles 1971*b*) and of *Ctenurella*. Thus two principal ossification centres in Meckel's cartilage, one anterior and one posterior, are probably synapomorphous for a group containing acanthodians, placoderms and osteichthyans, and furthermore these two centres presumably correspond to the hypobranchial and ceratobranchial ossification centres.

2. *Dermal bones*

The dermal bones of the lower jaw are more numerous in primitive actinopterygians than in later teleosts. The outer surface of the jaw is composed of two dermal bones in *Polypterus, Cheirolepis* and *Mimia*. These bones, in sequence the angular and the dentary, are canal-bearing. In many palaeoniscids and primitive neopterygians there is a third bone, the supra-angular, lying dorsal to the angular, sandwiched between it and the back of the dentary. On the inner surface of the jaw there is a further coronoid series, which in *Mimia* and *Moythomasia* comprises a prearticular (double in *Moythomasia*) and four coronoids, and in *Polypterus* a prearticular (= splenial) and two coronoids. A similar dermal bone pattern is encountered in most palaeoniscids (*Pteronisculus*, prearticular, three coronoids), *Ospia* (prearticular, two coronoids), *Lepisosteus* (prearticular, two coronoids), *Atractosteus* (prearticular, three coronoids) and *Amia* (prearticular, five coronoids). Pearson & Westoll (1979) record a supra-angular in *Cheirolepis* based on a single specimen (RSM 1877.30.5, figs 10b, 11e), but the bone in question is more probably a branchiostegal ray.

Neither a supra-angular nor a coronoid series is present in any living teleost (Nelson 1973); in sturgeons the only dermal ossifications are a prearticular and a dentary whereas in *Polyodon* only the dentary is present. The mandibular canal does not penetrate the dentary in *Polyodon* and is missing altogether in sturgeons.

Coronoids are present in halecomorphs, *Pachycormus, Ichthyokentema* and *Pholidophorus higginsi*, but absent in other pholidophorids and in leptolepids (Patterson 1977*a*). A supra-angular and a prearticular are present in all of these apart from leptolepids other than *Proleptolepis* (Patterson & Rosen 1977: fig. 32A), which retains a supra-angular. Both bones are missing in Recent teleosts. In advanced teleosts the angular and articular bones are co-ossified (Patterson 1977*b*), but in some leptolepids they fuse during ontogeny, as do the mentomeckelian bone and coronoids of *Mimia* and *Moythmasia*.

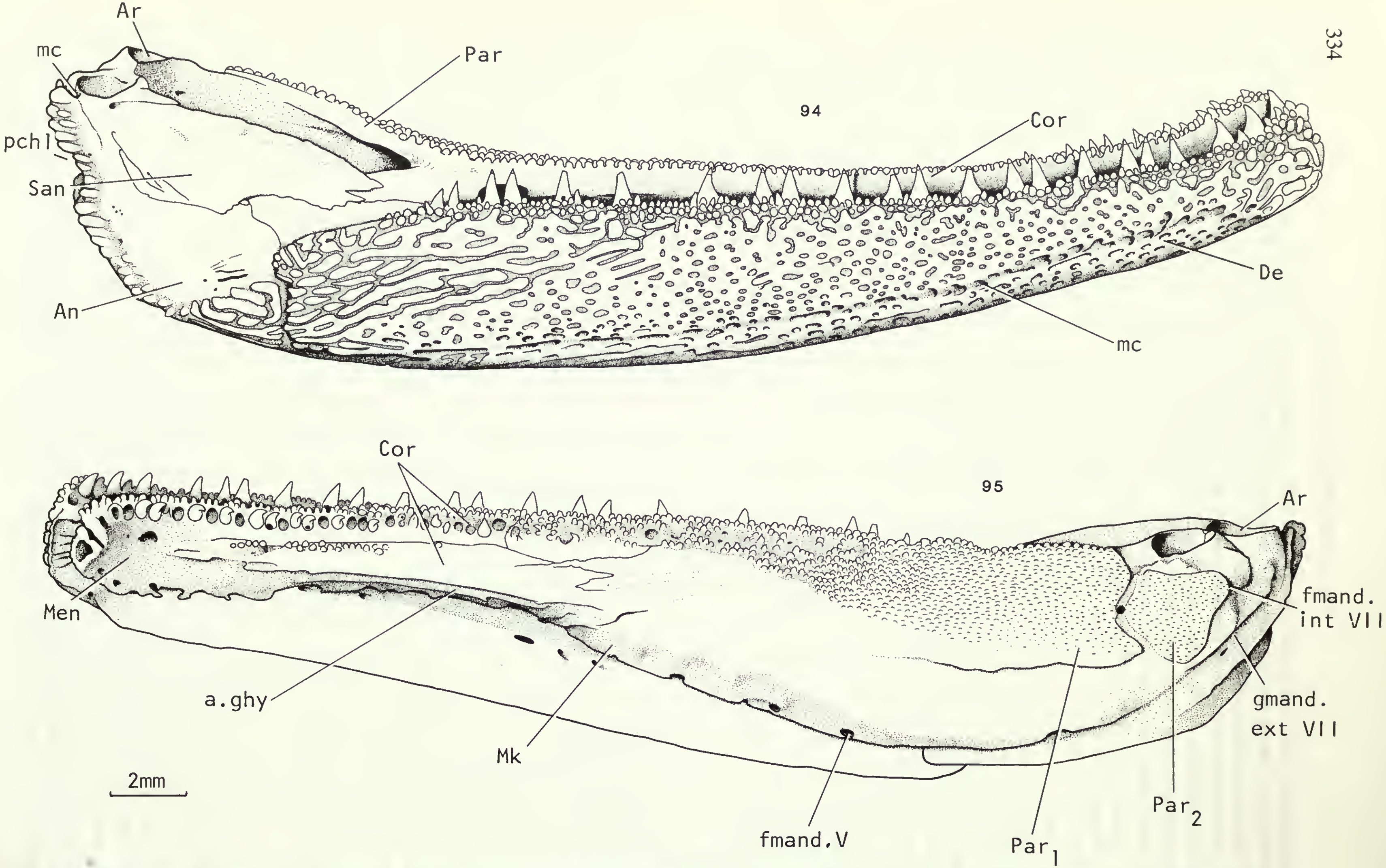
From this analysis I conclude, like Patterson (1982), that the supra-angular has been acquired within the actinopterygians and is primitively absent in *Cheirolepis, Polypterus* and *Mimia*.

The presence of a mandibular sensory canal within the dentary bone is unique to actinopterygians (Stensiö 1947). In other osteichthyans this canal runs through an independent splenial series. The splenial series consists of several bones, two in actinistians, four in osteolepiforms, porolepiforms, onychodonts, primitive dipnoans and early tetrapods. The single canal bone (angular) in actinopterygians must be part of this series. The splenial series, from the back forwards, are termed surangular, angular, splenial (postsplenial) and presplenial. The surangular is a canal-bearing bone and is therefore unlikely to be homologous with the actinopterygian supra-angular (Nelson 1973). It carries the mandibular canal and part of the oral canal in osteolepiforms (*Eusthenopteron*, Jarvik 1947) and porolepiforms (*Holoptychius*, Jarvik 1972). In Devonian dipnoans it carries the oral canal and in primitive tetrapods such as temnospondyls (Nilsson 1943, 1944) and anthracosaurs (Panchen 1972, 1977) it is grooved by both the mandibular and oral canals. In actinistians such as *Rhabdoderma* (Forey 1981) and *Latimeria* the posterior bone, which embraces the articular, is called the angular, yet it contains both the mandibular sensory canal and the oral pit-line, much as does the angular in *Mimia* and *Polypterus*. Thus I conclude that the angular of actinopterygians and actinistians is topographically homologous with the surangular of *Eusthenopteron, Holoptychius*, dipnoans and tetrapods. Furthermore, the large bone at the back of the lower jaw in later dipnoans (cf. *Neoceratodus*) is better interpreted as a surangular (in the traditional sense) rather than an angular as Thomson & Campbell (1971) and Miles (1977) have regarded it.

In actinistians the large 'angular' is followed by a small splenial and a very small dentary. The dentary, in all but the Devonian forms, bears separate toothplates. There are five coronoids and a large prearticular in *Latimeria*; three of the coronoids lie above the prearticular. In *Macropoma* and *Whiteia* (P. L. Forey, personal communication) there are four coronoids, a large one above the prearticular and three anterior to it. In onychodonts there is a single coronoid with a whorl of teeth much as on the anterior coronoid of *Holoptychius*.

The lower jaws of *Eusthenopteron* and *Holoptychius* (Jarvik 1972) are very similar, and the dentary reaches the articular to form the dorsal margin of the adductor fossa, as in *Cheirolepis*. There are four coronoids, three lying above the prearticular and one anterior to it (parasymphysial plate of Jarvik 1972).

The dipnoan dentary is reduced in size, as in actinistians (Miles 1977: 217) and there is a single median toothplate at the symphysis (adsymphysial plate, Miles 1977). A median adsymphysial plate is an apomorphy of dipnoans. In *Neoceratodus* larvae there is also a separate coronoid on either side of the adsymphysial plate (Semon 1899: pl. 20). The surangular usually forms the margin of the adductor fossa, as in actinistians and tetrapods, and the oral canal passes through the surangular into the dentary in *Chirodipterus, Holodipterus* and *Dipnorhynchus*. A full oral line is found in acanthodians, chondrichthyans such as *Chlamydoselachus*, dipnoans and amphibians (Stensiö 1947) and is probably a primitive gnathostome character. But only in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Figs 94–95 *Moythomasia durgaringa* Gardiner & Bartram. Right lower jaw, from BMNH P.53221. Fig. 94, lateral view. Fig. 95, medial view.

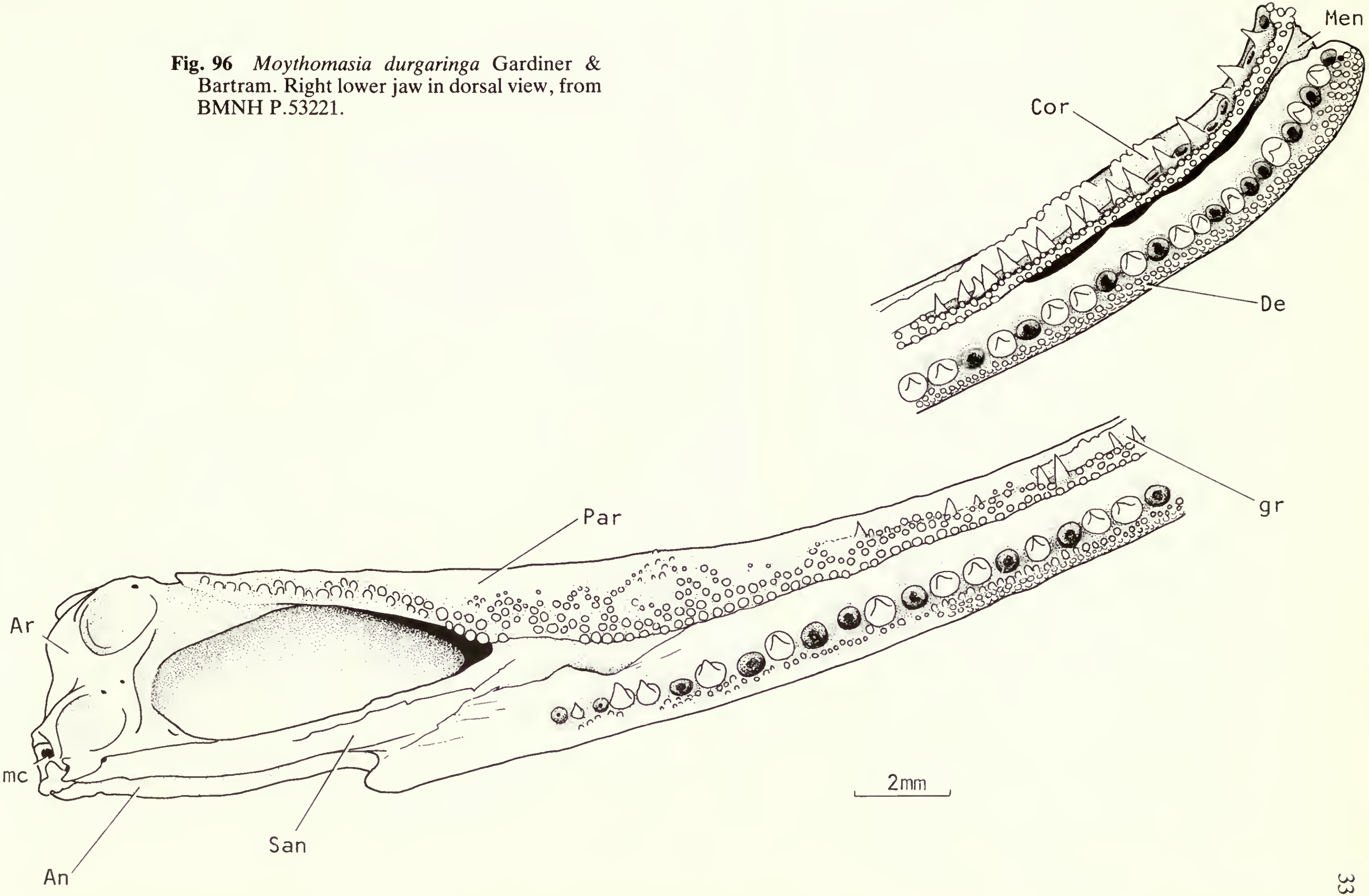
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Fig. 96 *Moythomasia durgaringa* Gardiner & Bartram. Right lower jaw in dorsal view, from BMNH P.53221.

dipnoans and tetrapods (Nilsson 1943, 1944, Panchen 1972) is it ever associated with the dentary. The lower jaws of temnospondyls and anthracosaurs possess three coronoids, but those of Lissamphibia are characterized by the absence of the splenials and angular (= surangular of most authors). The lower jaw of anthracosaurs is characterized by two large meckelian fenestrae, separated by the postsplenial bone.

In acanthodians the ventral margin of Meckel's cartilage frequently sits in a groove along the dorsal margin of the so-called mandibular bone (styliform process of Hancock & Atthey 1869; extramandibular spine of Reis 1890, 1895). The lateral surface of this bone is often ornamented (Miles 1966), confirming its dermal origin. The medial surface of the dentary of *Polypterus* is similarly deeply grooved along its entire length. The mandibular bone stretches the whole length of Meckel's cartilage in *Acanthodes* (and projects anteriorly beyond it in many specimens) but in *Mesacanthus* it is relatively shorter. It has been homologized with the splenials of osteichthyans (Jaekel 1899, Dean 1907) and temnospondyls (Stensiö 1947). A mandibular bone is present in many members of the Diplacanthidae, Ischnacanthidae and Acanthodidae, but its absence in certain Devonian Acanthodidae and the Lower Devonian *Ischnacanthus* has prompted Denison (1979) to consider this the primitive condition. The mandibular canal runs ventral to the mandibular bone; nevertheless from its topographic position, stretching as it does from the articular to the end of the mentomeckelian, it is better homologized with the splenial of osteichthyans than with the dentary. From its distribution with the acanthodians I consider it synapomorphous for a group containing acanthodians and osteichthyans. Both Miles (1971*a*) and Denison (1979) considered the function of the mandibular bone was to stiffen the Meckelian cartilage.

Teeth when present in acanthodians occur in three forms; as single teeth, spirals or whorls, or fused to dermal jaw bones (Denison 1979). Thus numerous small, single teeth were situated in the lining of the mouth of many ischnacanthids and there was a well-formed, large, lower median symphysial tooth whorl (cf. *Chlamydoselachus*). Mandibular toothplates are also found in many ischnacanthids and Denison (1979) proposed that these are a unique derived character of Ischnacanthidae. Many attempts have been made to elucidate the structure of these toothplates (Ørvig 1957, 1967*a*, 1973; Gross 1957; Miles 1966) and it is now generally agreed that they consist of tooth-cusps anchylosed to a supporting bony base. There is no clear boundary between the dentinous tissue of the teeth and the basal bone tissue. The teeth are described as stephanodont (Jaekel 1919) and said to be composed of dentine or dentinous tissue (Ørvig 1973). The underlying bone may be cell-bearing or acellular, fairly dense with vascular canals or cancellous. The teeth are arranged in one or more longitudinal rows and are frequently worn by use. In specimens of *Nostolepis* there are worn tooth-cusps alternating with shearing edges formed by the abraded rows of side-cusps (Ørvig 1973). As in placoderms these worn teeth are never replaced by subsequent teeth in the same positions. The principal tooth-cusps in *Nostolepis* are said to be made up of an external layer of pallial dentine (Gross 1957) or pallial mesodentine (Ørvig 1973). The side cusps of the multicuspidate teeth of *Nostolepis* also consist of mesodentine. The cores of the teeth are of osteodentine and osteomesodentine. Mesodentine is also said to be present in osteostracans (Ørvig 1967*a*).

In rhenanid placoderms the outer face of the palatoquadrate and Meckelian cartilage is covered by small tesserae with stellate tubercles, in stensioellids by small denticles, and in pseudopetalichthyids by small scale-like plates. Dermal jaw bones are unknown in Acanthothoraci, Petalichthyida and Phyllolepida, but Ptyctodontida, Arthrodira and Antiarcha have well-developed dermal jaw bones (Denison 1978). In arthrodires there is a large dermal toothplate or inferognathal associated with the Meckelian cartilage. Anteriorly in *Eastmanosteus* (Gardiner & Miles 1975) the inferognathal sits over the perichondral mentomandibular, but posteriorly it rests on the medial surface of the articular. The inferognathals in branchythoracids carry teeth (Zahntuberkeln of Gross 1957) which are continuous basally with the adjoining bone tissue and may therefore be considered stephanodont as in acanthodians (Jaekel 1919). These teeth are simply cusps on the bone surface which become worn away during life (Miles 1971*a*). New teeth are said to be added to one end of a tooth row as the gnathals grow at their bases. The teeth consist externally of semidentine surrounding an osteosemidentine core. In some arthrodires (*Sedowichthys, Mylostoma*, Ørvig 1967*a*, 1973) and the acanthothoracid *Romundina*, the thickened ridges consist of mesodentine, as in many acanthodians. On abraded plates the osteosemidentine is said to have worn away and the biting area to consist of dense bone. The most prominent teeth in arthrodires are seen on the superognathal of the phlyctaeniid *Dicksonosteus*, where they are very markedly tubercular. In antiarchs the inferognathals have a broad biting anterior portion and a slender posterolateral ramus.

In ptyctodonts there is a large crushing or sectorial toothplate. This plate may have a shearing edge, as in *Rhamphodopsis*, or a large central tritural area, as in *Ptyctodus*, or separate tritural cusps as in *Palaeomylus* (Miles 1971*a*). These toothplates all have dense bone beneath and are strengthened by inwardly-growing hypermineralized columnar tissue (secondary dentine of Gross 1957; osteosemidentine of Ørvig 1973) which in *Ptyctodus* forms the tritural areas as the outer layers of normal dentinal tissue become won away. A similar columnar tissue is developed in brachythoracid arthrodires, in holocephalans and in dipnoans (Miles 1971*a*, Ørvig 1973). In arthrodires and ptyctodonts the osteosemidentine is surrounded by semidentine and occasionally by mesodentine. In some ptyctodonts the gnathals have an outer layer of orthodentine and an inner mass of trabecular dentine. In this latter respect and in the similar presumed growth pattern of the stephanodont teeth, placoderms resemble acanthodians

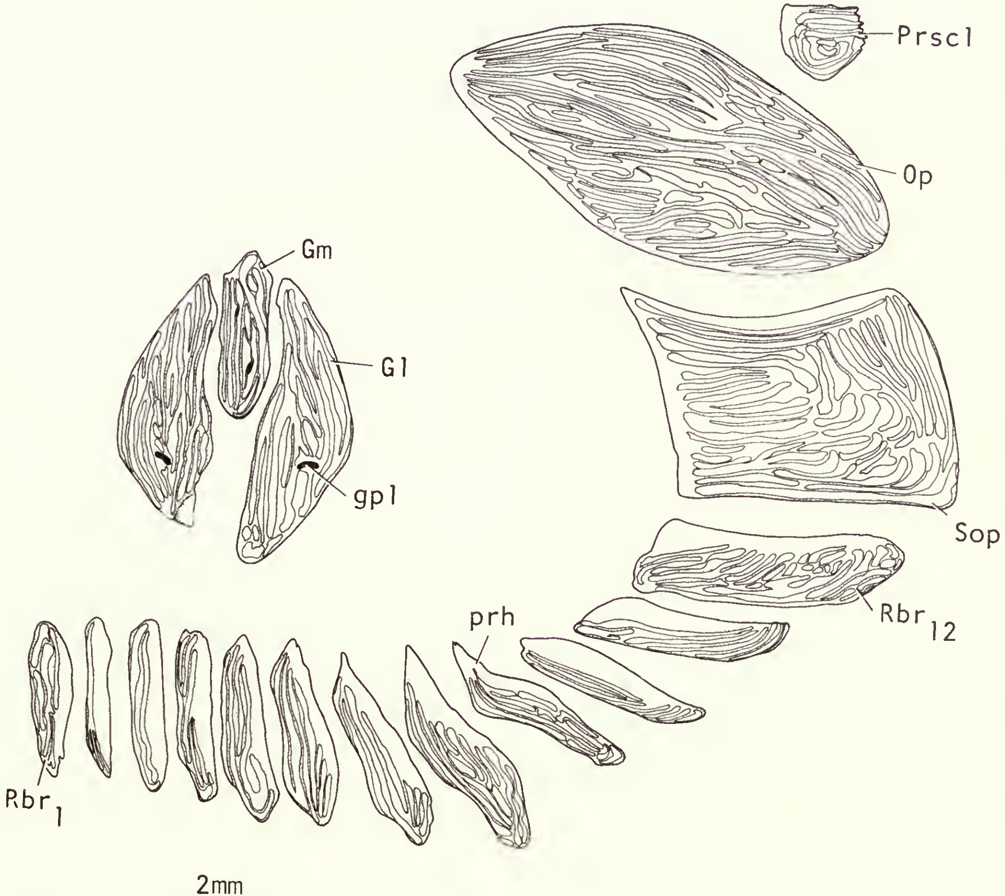

Fig. 97 *Mimia toombsi* Gardiner & Bartram. Opercular, branchiostegal and gular bones and presupracleithrum, drawn as if folded out in one plane, from BMNH P.56495.

(Ørvig 1973). In holocephalans the dermal toothplates arise as whole units in the dermis of the jaws, but in *Neoceratodus* (Kemp 1977) the plates develop from simple groups of isolated cusps which eventually fuse in ridges. All this evidence suggests either that dermal toothplates associated with the dorsal surface of the Meckelian cartilage are a primitive feature of gnathostomes, or that they have been independently developed in holocephalans and in acanthodians, placoderms and osteichthyans. The latter view is the more parsimonious.

The only other dermal bones said to be associated with the lateral and ventral faces of the Meckelian cartilage are the infraprelateral and mandibular plate(s) found in *Bothriolepis* (Stensiö 1931, 1948, Denison 1978). In a specimen of *Bothriolepis* (BMNH P.50898) demonstrated to me by R. S. Miles, the infraprelateral is sutured to the prelateral and is clearly part of the cheek, and the remaining mandibular plate(s) described by Stensiö (1931, 1948) are too incompletely known to comment on.

Operculogular series

Mimia toombsi

The opercular is four-sided with a convex posterior margin. Ventrally it overlaps the dorsal margin of the subopercular. The centre of radiation of the opercular lies in the anterodorsal corner. Internally, just below this centre, there is a small cup-shaped depression (see *Moythomasia*, dop, Fig. 99) which as in *Polypterus* (Allis 1922: pl. 11; fig. 33) is presumed to have housed an opercular cartilage.

The subopercular is rectangular and its radiation centre is near the anterior margin. The anterior margin fitted beneath the posterior edge of the preopercular and did not articulate with the hyomandibula as it is said to have done in *Pteronisculus* (Nielsen 1942).

There are twelve branchiostegal rays which diminish in size anteriorly, each ray overlapping the one posterior to it. Several of the branchiostegal rays have a pronounced anterior projection

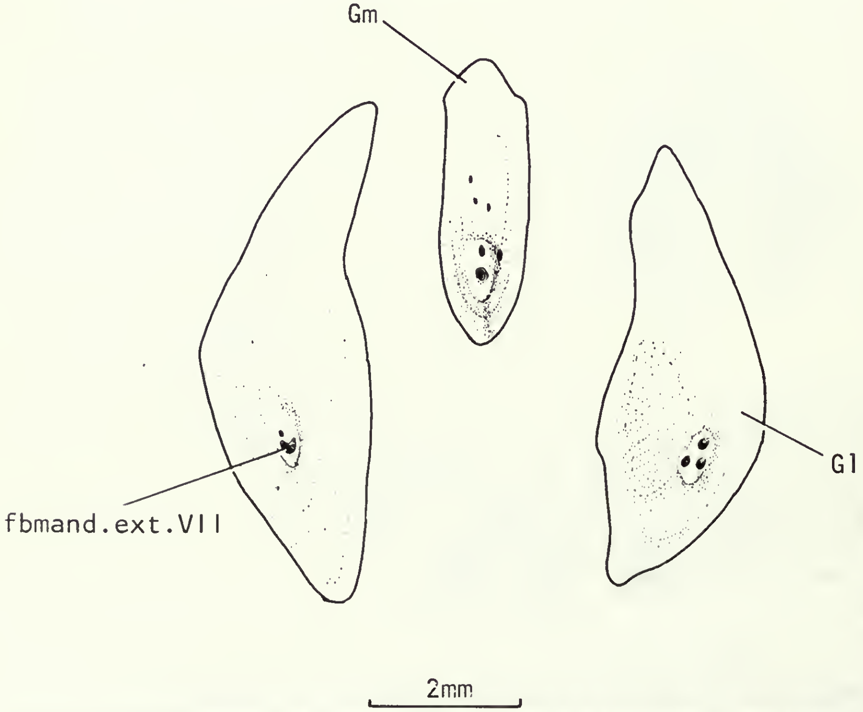

Fig. 98 *Momia toombsi* Gardiner & Bartram. Gular plates in dorsal view, from BMNH P.56495.

(hyoid process) devoid of ornament (prh, Fig. 97), which is also seen in *Cheirolepis* (Pearson & Westoll 1979: 363) and may have been inserted along the ceratohyal as in Recent forms. The first branchiostegal ray, although somewhat larger than the second, neither overlapped nor underlay the lateral gular. The lateral gulars are much larger than the preceding branchiostegal rays. Posteriorly the left lateral gular overlaps the right. The rhombic median gular in turn overlaps the anterior medial edges of the lateral gulars. The radiation centres of the three gulars lie near the centres of the bones, immediately beneath the pit-line; those of the branchiostegals lie much nearer their mandibular margins. Each gular has a slot-shaped pit-line (gpl, Fig. 97) in the form of an arc. On the internal surface there is a corresponding cluster of foramina for branches of the external mandibular nerve (fbmand.ext. VII, Fig. 98). Similar pit-lines are present on the lateral gulars of *Polypterus* (Pehrson 1947, Jarvik 1947) and *Pteronisculus* (Nielsen 1942), and on the median gular of *Amia*.

It will be convenient to deal with the presupracleithrum (Nybelin 1976) at this point. This bone lies behind the posterodorsal corner of the opercular, posterolateral to the supracleithrum. It is overlapped anteriorly by the opercular. In *Polypterus* a similar bone, the posterior postspiracular, overlaps the dorsal edge of the opercular, which is slightly grooved for it. The same bone is present in many palaeoniscids (*Cheirolepis, Pteronisculus, Boreosomus*) and other fossil actinopterans, where it has also been called the postspiracular bone (Nielsen 1942: 182). The presence of a presupracleithrum is considered a synapomorphy of actinopterygians.

Moythomasia durgaringa

Moythomasia differs little from *Mimia*. The opercular is more lozenge-shaped and the subopercular is deeper than wide. The median gular is kite-shaped and has a V-shaped pit-line similar to that of *Amia*.

Operculogular series: summary and discussion

1. *Branchiostegal rays and gular plates*

Numerous long branchiostegal rays are found in many primitive actinopterygians. There are 12 in *Cheirolepis, Mimia* and *Moythomasia*, 20 in *Cosmoptychius* and more than 30 in *Tegeolepis*. In *Polypterus* there are no branchiostegal rays and *Polyodon* has only a single pair. *Lepisosteus* has three rays, *Amia* 11 and in higher teleosts there are rarely more than eight. The lateral gulars are in series with the branchiostegal rays and together with the median gular fill the area between the jaw rami. All three gulars occur in the most primitive actinopterygians, including *Cheirolepis, Mimia, Pteronisculus* and *Haplolepis*. *Boreosomus* has only median gulars (one or two, Nielsen 1942: 349) and *Polypterus* only lateral gulars. Gulars are missing altogether in sturgeons, paddlefishes, *Lepisosteus* and most teleosts, but a median gular is present in *Amia*, pachycormids, pholidophorids, leptolepids, elopids and albulids.

Actinistians (cf. *Diplocercides, Rhabdoderma, Latimeria*) resemble cladistians in possessing a single pair of lateral gulars and having no branchiostegal rays.

In osteolepiforms, porolepiforms, onychodonts and dipnoans there is an operculogular series with lateral and median gulars as well as a so-called submandibular series. Miles (1977: 258) and Patterson (1982) consider the submandibular series to be a specialization of dipnoans and rhipidistians; Patterson (1982) regards the submandibulars as shortened branchiostegal rays. Jarvik (1963), however, considered them to be part of a mandibular gill-cover and therefore not homologous with branchiostegal rays. Jarvik (1968, 1972) further argued that the primitive gnathostome possessed both series of bones, submandibular and branchiostegal.

In osteolepiforms such as *Eusthenopteron* there are eight submandibular bones with the anterior members of the series intercalated between the gular and the mandible. There are paired lateral gulars and a small median gular similar in size to those in primitive actinopterygians.

In porolepiforms (*Porolepis, Glyptolepis, Holoptychius*, Jarvik 1972) there are 9–10 submandibulars and very large lateral gulars. The lateral gulars are large in actinistians (*Diplocercides, Rhabdoderma*) and cladistians. There may be two median gulars (*Porolepis*) or none (*Holoptychius*). The anterior median gular in *Porolepis* does not carry a pit-line and is best

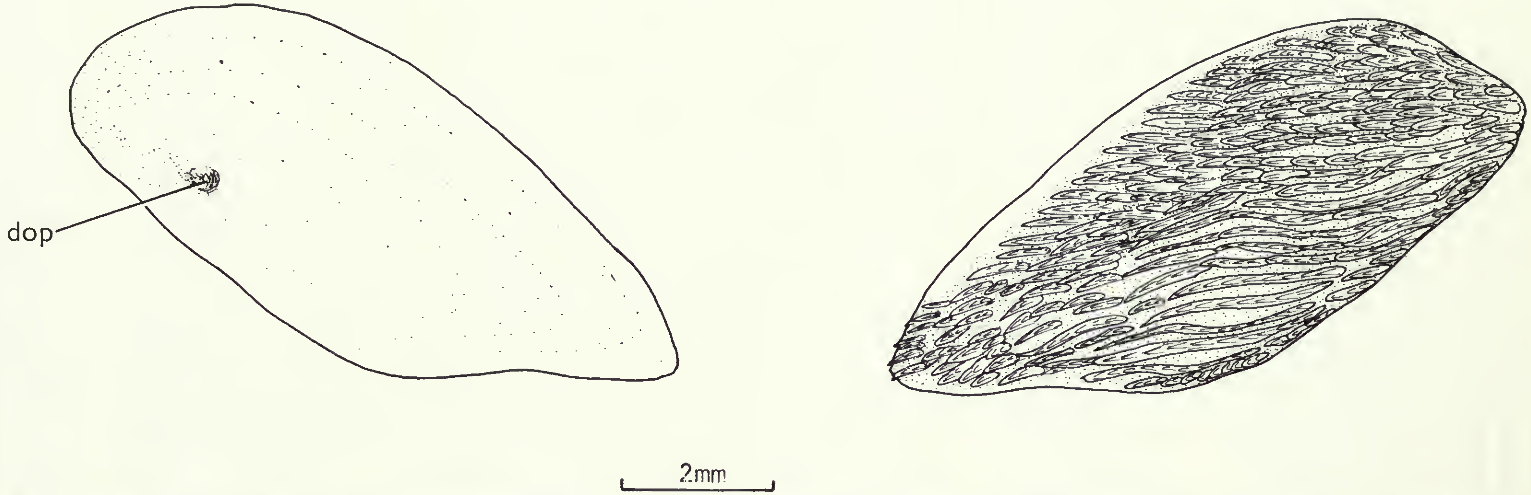

Fig. 99 *Moythomasia durgaringa* Gardiner & Bartram. Right opercular in medial (left) and lateral views, from BMNH P.56480.

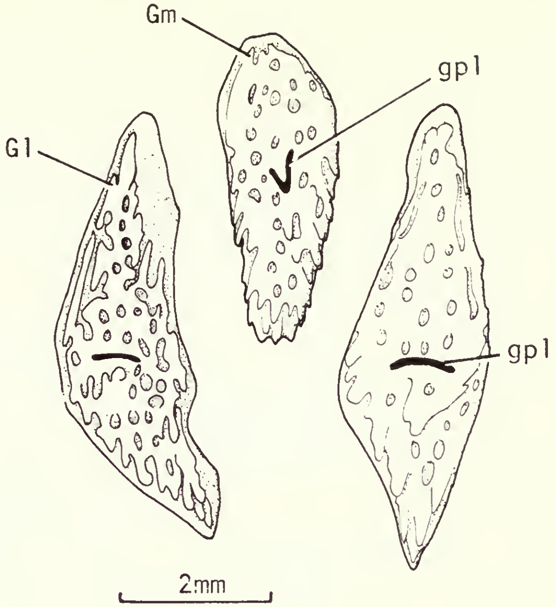

Fig. 100 *Moythomasia durgaringa* Gardiner & Bartram. Gular plates in ventral view, from BMNH P.56480.

homologized with the median submandibular of dipnoans (Jarvik 1967*a*) and the anterior median gular of *Boreosomus* (Nielsen 1942: fig. 73). The posterior median gular carries a pit-line in both *Porolepis* and *Chirodipterus* (Miles 1977: figs. 105, 129, sbm.m).

In fossil dipnoans the submandibulars vary greatly in size and shape. The most posterior member (subopercular plate 2 of *Griphognathus*, Miles 1977; posterolateral gular of *Scaumenacia*, Jarvik 1967*a*) looks like a branchiostegal ray, whereas the most anterior (principal submandibular) resembles the lateral gulars. Between them is a short, triangular lateral submandibular (Jarvik 1967*a*: fig. 5B; Miles 1977: fig. 126). There are usually three submandibulars in dipnoans (*Griphognathus, Chirodipterus, Scaumenacia*), counting the anterior gular-like pair, but *Rhinodipterus* may have more. If submandibulars are shortened branchiostegal rays then the anterior (principal) submandibulars are more parsimoniously interpreted as anterior lateral gulars and as a synapomorphy of dipnoans. Neither an operculogular series nor branchiostegal rays is present in tetrapods.

In the placoderm *Bothriolepis*, Stensiö (1931, 1948) described a fragmentary series of dermal bones which he suggested were associated with the lower jaw and the hyoid gill cover. These have not been described in any other placoderm; nevertheless Jarvik (1968, 1972) has suggested that some of these elements may belong to the submandibular series. The bones in question do not in my estimation form a recognizable series. Elsewhere in placoderms there is a distinct hyoid gill cover in the form of a dermohyal (submarginal, middle preoperculum, extralateral), which is fused to the head of the hyomandibula in phlyctaeniids (Goujet 1975: fig. 4) and coccosteids (Miles 1971*b*: fig. 111). The inner surface of the dermohyal is also attached to the opercular cartilage in *Holonema* (Miles 1971*b*). In some Pachyosteina (*Pachyosteus, Brachyosteus*) the dermohyal is incorporated into the head shield. A large dermohyal is found in rhenanids (*Gemuendina*, Gross 1963; *Jagorina*, Stensiö 1969), pseudopetalichthyids (*Pseudopetalichthys, Paraplesiobatis*, Gross 1962), petalichthyids (*Lunaspis*, Gross 1961) and arthrodires.

The association of the dermohyal with the hyomandibula in placoderms and actinopterygians forces me to regard the dermohyal as a synapomorphy of a group including placoderms and actinopterygians.

In acanthodians, branchiostegal rays are widespread with up to 25 overlapping rays in *Euthacanthus* and *Mesacanthus* (Watson 1937), and 10 or fewer in *Climatius* and

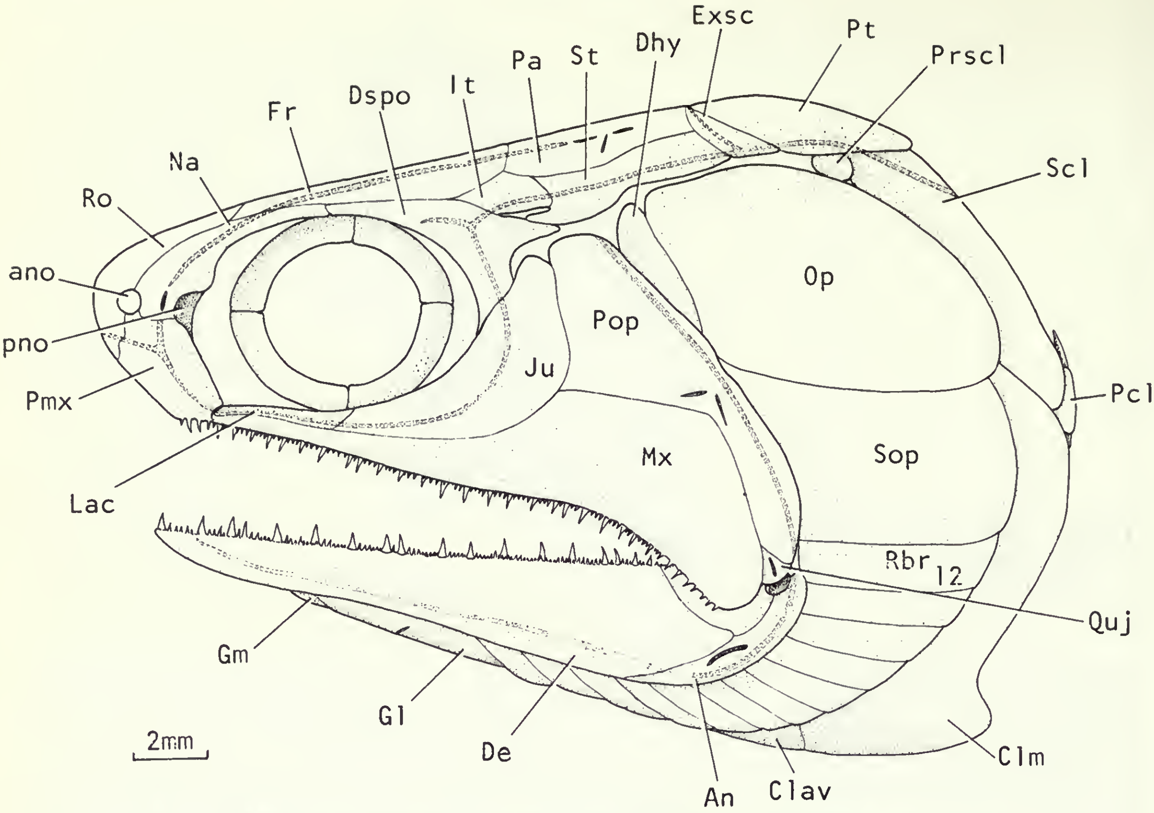

Fig. 101 *Mimia toombsi* Gardiner & Bartram. Restoration of skull in lateral view.

Brachyacanthus. In *Homalacanthus* (Miles 1966) there are some 17 widely-spaced rays behind the 'preopercular' and in *Acanthodes* there are more than 20 very weak rays associated with the ceratohyal (Miles 1973*a*: pl. 6). In this latter genus they are too short to have covered the gills completely.

In summary, long branchiostegal rays are found in the hyoid operculum of acanthodians and actinopterygians and, as Patterson (1982) has argued, must be synapomorphous for a group containing acanthodians and actinopterygians. The anterior branchiostegal rays are in series with the lateral and median gulars in primitive actinopterygians, and gular plates are considered to be a synapomorphy of osteichthyans. Shortened branchiostegal rays (submandibulars) which have lost all contact with the certohyal are regarded s synapomorphous for carcopterygians.

2. *Opercular cartilages and opercular bones*

An opercular and subopercular are found in almost all non-tetrapod osteichthyans, where they are generally believed to be enlarged branchiostegal rays.

Opercular cartilages are found in chondrichthyans, placoderms and osteichthyans. In selachians there are numerous hyoid ray cartilages and in *Scyllium*, for example, three are associated with the hyomandibula. In chimaeroids a single large opercular cartilage supports the opercular rays. A single large opercular cartilage is also characteristic of such diverse placoderms as *Jagorina, Brindabellaspis* and *Bothriolepis*, and in *Holonema* it helps support a dermohyal.

Opercular cartilages are spasmodically distributed throughout actinopterygians. Thus, a small opercular cartilage is seen in larval *Polypterus* and *Anguilla*, and in the adult *Polypterus* it lines the articular facet of the opercular bone as in *Heterotis* and *Elops* (Patterson 1977*b*: 90). In

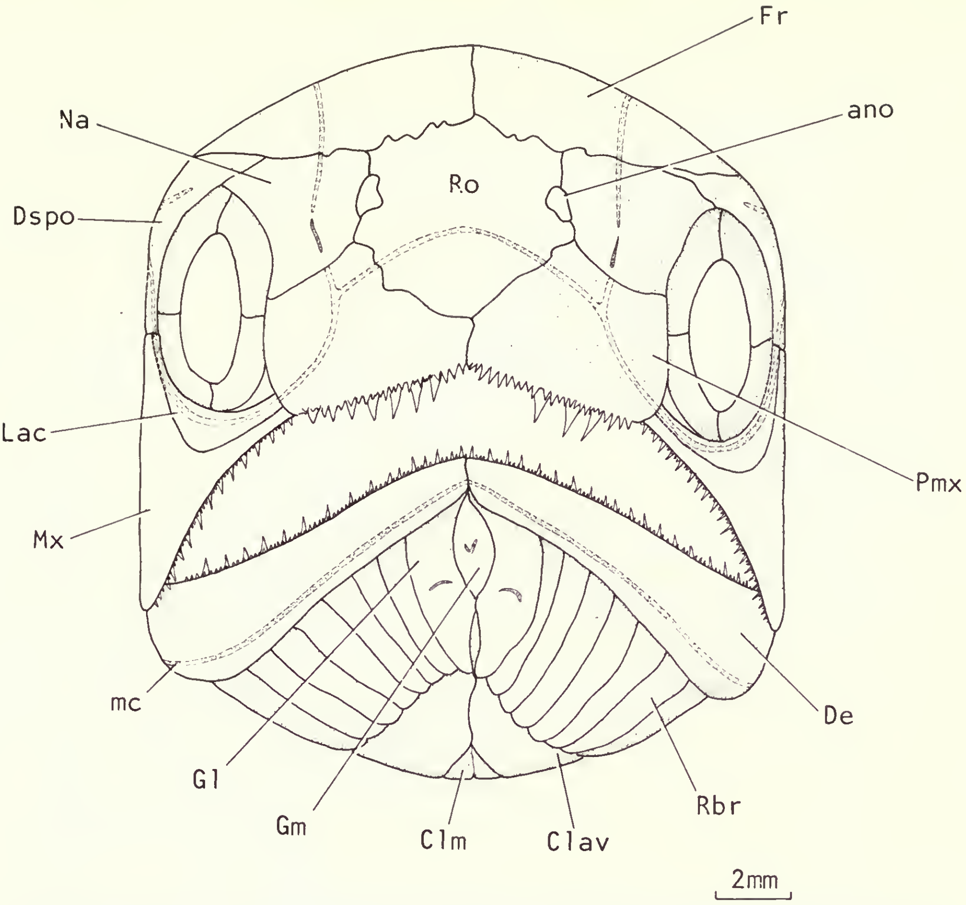

Fig. 102 *Mimia toombsi* Gardiner & Bartram. Restoration of skull in anterior view.

adult *Anguilla* (Norman 1926: 298), on the other hand, the opercular cartilage only contacts the dorsal margin of the opercular. A large opercular cartilage occurs in several teleosts including saccopharyngoids (Harrisson 1966: 451).

Latimeria also possesses a large opercular cartilage (Millot & Anthony 1958) which contacts the ventroposterior margin of the opercular. In *Lepidosiren* and *Neoceratodus* (Bridge 1898) there are two opercular cartilages, one attached to the posterior inner surface of the opercular and the other to the posterior inner surface of the subopercular.

Opercular cartilages are unknown in acanthodians. An opercular and a subopercular are believed to be synapomorphous for osteichthyans.

In halecostomes (*Amia*, teleosts) there is an additional bone in the operculogular series, the interopercular. Although out of line with this series the interoperocular is probably a modified branchiostegal ray and is considered synapomorphous for halecostomes (Patterson 1973). (Re-examination of *Platysiagum* has convinced me that the bone identified as an incipient interopercular by Brough (1939) and an interopercular by me (Gardiner 1960) is no more than a displaced branchiostegal ray.)

A further ossification, structurally part of the operculum, is often found in the anterodorsal corner. This bone is referred to either as the antopercular or as the postspiracular (Nielsen 1936: 42). A single antopercular is present in *Pteronisculus, Commentrya, Brachydegma, Pygopterus, Perleidus* and *Redfieldius* and in the osteolepiform *Eusthenopteron*. Two antoperculars are found in *Boreosomus, Platysiagum* and *Polypterus*.

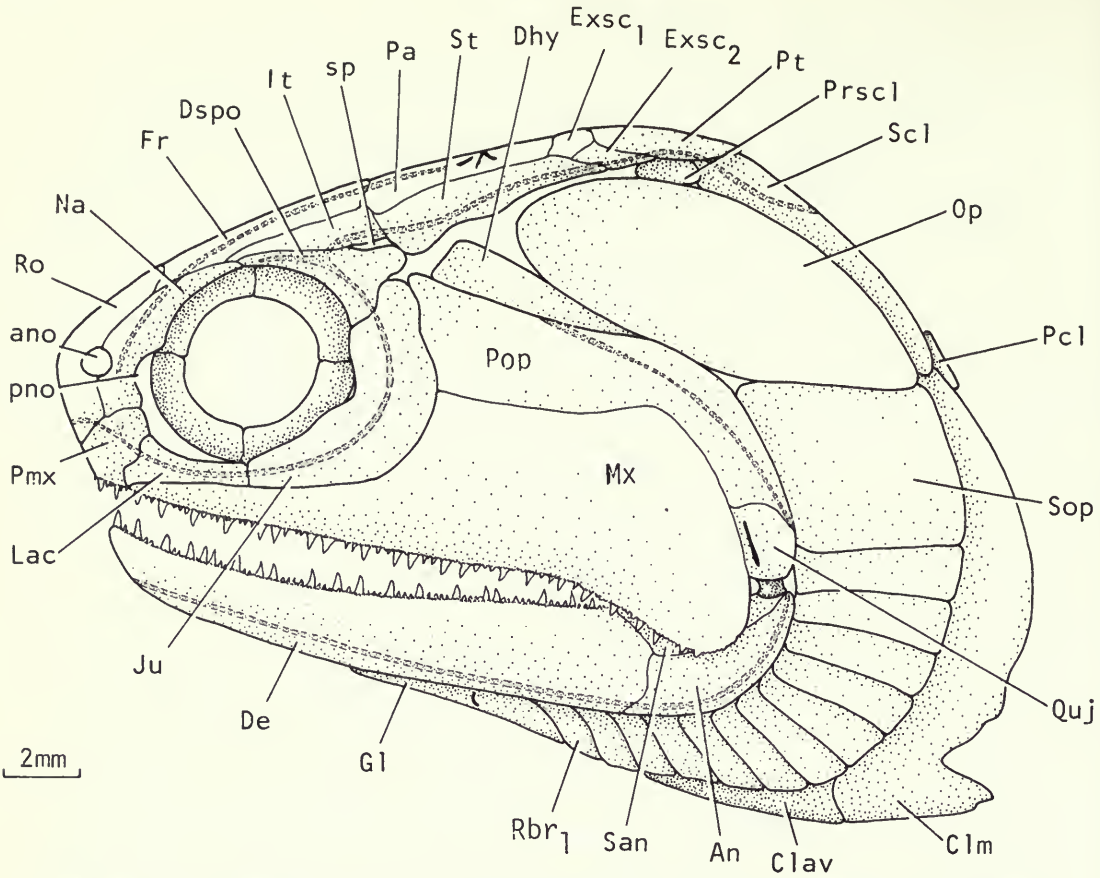

Fig. 103 *Moythomasia durgaringa* Gardiner & Bartram. Restoration of skull in lateral view.

A few primitive actinopterygians also possess accessory operculars in the anteroventral corner of the operculum: these include *Cheirolepis, Watsonichthys, Cosmoptychius, Kentuckia* and *Gonatodus*.

Hyoid and branchial arches

Mimia toombsi

The hyoid arch includes a hyomandibula, dermohyal, interhyal, ceratohyal and hypohyal.

The hyomandibula is a large, stout, gently curved bone which articulates dorsally with the otic region of the neurocranium. Distally it articulates with the interhyal. The hyomandibula is a solid structure of endochondral bone with a small triangular dermohyal intimately fused with its dorsal shank (Pl. 1; Fig. 104). In cross section it is rounded laterally, but medially a well-marked gutter runs across the bottom of the dorsal shank and continues ventrally to the posterior margin. Toothplates clothe the anteromedial surface in front of the gutter, while much smaller plates occur on the anterior margin of the dorsal shank. The disposition of these toothplates is very similar to that described for *Eusthenopteron* by Jarvik (1954: fig. 16A, B). A perichondrally-lined canal (chy, Fig. 104) passes obliquely down through the hyomandibula in the ventrolateral direction. Medially a wide, shallow groove runs down into the mouth of this canal and laterally the canal opens into a shallow groove on the surface of the shaft, just below the dermohyal. This canal presumably transmitted the hyomandibular trunk of the facial nerve, as in *Amia* and *Lepisosteus*. Other surface features of the hyomandibula include a small

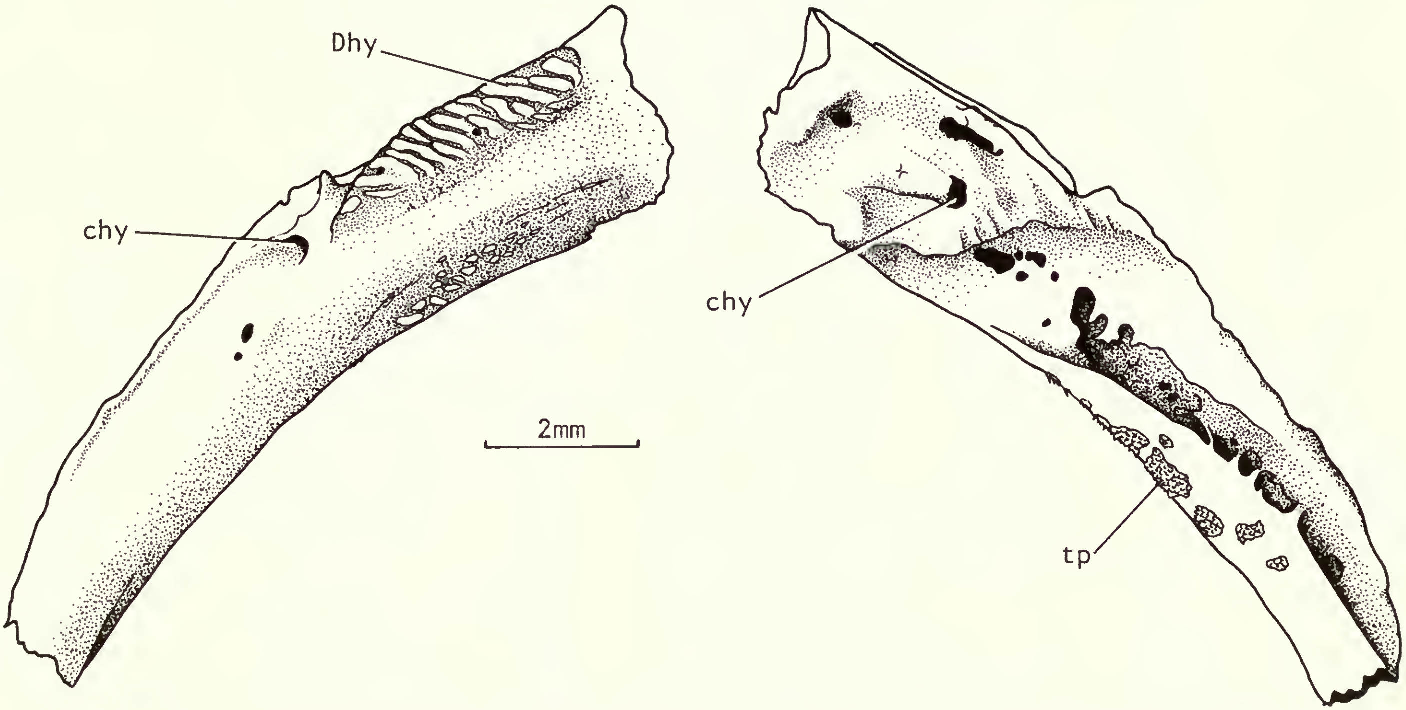
Dhy
chy
2mm
chy
tp

Fig. 104 *Mimia toombsi* Gardiner & Bartram. Right hyomandibula in lateral (left) and medial views, from BMNH P.56498.

projection or notch in the posterior margin near the ventral corner of the dermohyal. This notch may have transmitted the hyoid branch of the facial nerve, as in *Polypterus* (Allis 1922: pl. 17), and as postulated in other palaeoniscids by Stensiö (1925: 169) and in *Eusthenopteron* by Jarvik (1954: fig. 16A, B). However, the condition in *Polypterus* is unique; in all other osteichthyans where the nerve passes through the bone (*Amia, Lepisosteus*, generalized teleosts, *Latimeria*, larval *Neoceratodus*) it never divides into the mandibular and hyoid branches until it has pierced the hyomandibula (see also *Moythomasia*, Fig. 105). It therefore seems unlikely that it divided into its constituent branches prior to its passage through the hyomandibula in either *Mimia* or *Eusthenopteron*.

Both the interhyal and ceratohyal are perichondral shells lacking any endochondral ossification. The interhyal is a small, somewhat cylindrical bone, open at each end where it articulated with the lateral portion of the proximal end of the ceratohyal and the distal end of the hyomandibula (Fig. 108), much as in *Polypterus*. It does not articulate with either the palatoquadrate or the Meckelian cartilage, as it is said to do in *Pteronisculus* (Nielsen 1942: 175; fig. 42).

The ceratohyal is a stout, flat, slightly curved bone, expanded ventrally in its posterior third. On its lateral face there is a broad longitudinal groove (see *Moythomasia*, ahy, Fig. 106) for the afferent hyoidean artery. A similar groove has been reported in *Pteronisculus, Australosomus* (Nielsen 1949: fig. 37), *Plegmolepis, Pygopterus* (Aldinger 1937: figs 19, 41B) and *Eusthenopteron* (Jarvik 1954: 22; fig. 8A). A continuous toothplate runs along its dorsomedial margin (BMNH P.53245), as in *Elops*.

The hypohyal, like the ceratohyal, is a perichondral ossification, open at both ends. It is a flat, strongly curved bone which lies in the vertical plane, with its distal edge directed posteromedially to articulate with the anterior end of the basibranchial. A few small toothplates are found on the dorsomedial surface (Fig. 107). A stout ventral projection of the hypohyal presumably served for the insertion of the sternohyoideus muscle (cf. *Polypterus, Lepisosteus*).

Five branchial arches are present, each component of which consists of perichondral ossifications with a weak endochondral core. The individual ossifications are presumed to have articulated with one another by cartilaginous epiphyses. The elements are usually scattered, but there are enough specimens with parts of the arches in position to enable precise reconstructions to be made.

The first branchial arch consists of hypobranchial, ceratobranchial, epibranchial, infrapharyngobranchial and suprapharyngobranchial. The hypobranchial is a long, slender bone with an enlarged, inturned distal end which articulates with the anterior end of the basibranchial, immediately behind the hypophyal (Fig. 108). Thus the first hypobranchial and hypohyal share the same articular facet, as they do in *Pteronisculus* (Nielsen 1942: fig. 45) and *Australosomus* (Nielsen 1949: 121), and as they partly do in *Polypterus* (Allis 1922: pl. 8). Ceratobranchial 1 (Fig. 108) is a very long rod, strongly arched dorsoventrally. It is semicircular in section, with a deep, longitudinal groove on its ventral face (see *Moythomasia*, Fig. 115). The groove is presumed to have carried the afferent artery and branchial nerve, as in *Polypterus, Amia* etc. Proximally the edges of the ceratobranchial groove have closed up to form a foramen for the artery and nerve as in *Moythomasia* (fcb, Fig. 115). A similar foramen has been described in the Gogo dipnoan *Griphognathus* (Miles 1977: fig. 135). Two rows of toothplates cover the dorsomedial surface of both the hypobranchial and ceratobranchial. The ventromedial edge of the ceratobranchial is often regularly scalloped. The first epibranchial is about half the length of the ceratobranchial and has a deep longitudinal arterial groove in its posterior margin. Ventrally the lateral wall of the groove is produced posteriorly to form a partially covered canal. Dorsally the medial wall is developed as a dorsally-directed process for the articulation of suprapharyngobranchial 1. Toothplates clothe the lateral edge of the epibranchial and appear to be arranged in at least two rows (Fig. 116B). The first infrapharyngobranchial is a short, elbowed bone, which articulates with the anteriorly-directed proximal end of epibranchial 1 and with a ventral facet on the otic portion of the neurocranium. Ventrally it is covered by a row of small toothplates. The first suprapharyngobranchial is a flat bone, considerably larger than the infrapharyngobranchial. Posteroventrally it has a short process projecting beyond the articular

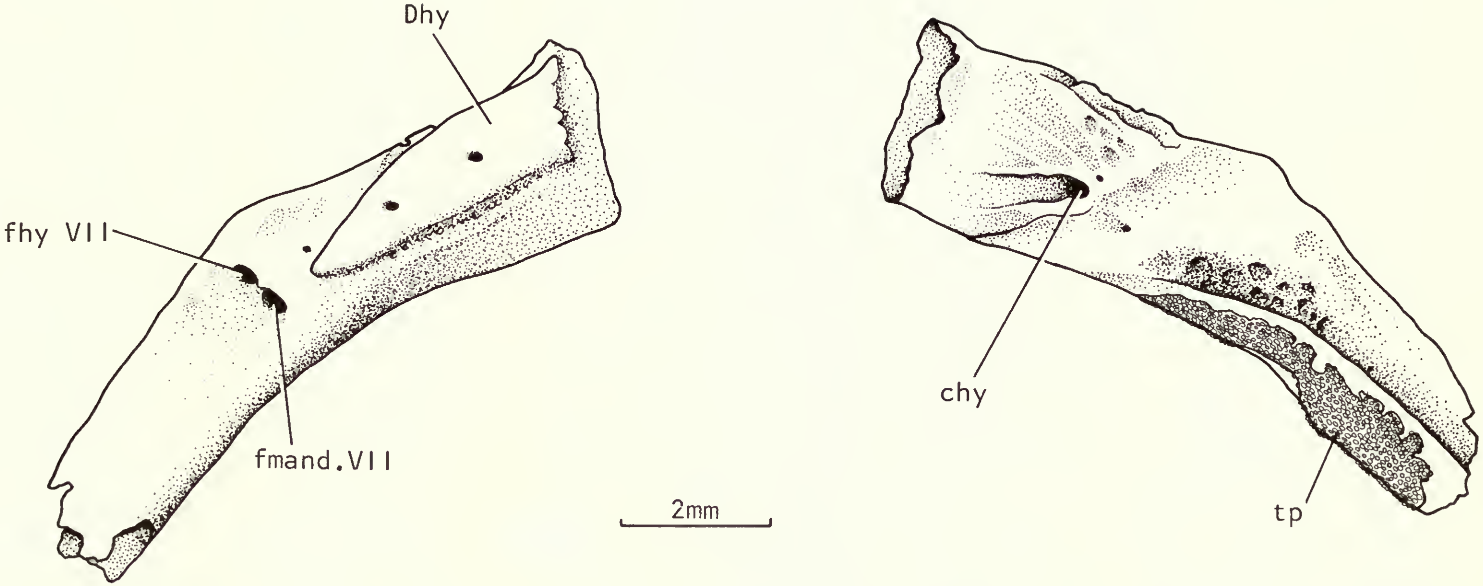
Dhy
fhy VII
fmand.VII
2mm
chy
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Fig. 105 *Moythomasia durgaringa* Gardiner & Bartram. Right hyomandibula in lateral (right) and medial views, from BMNH P.53255.

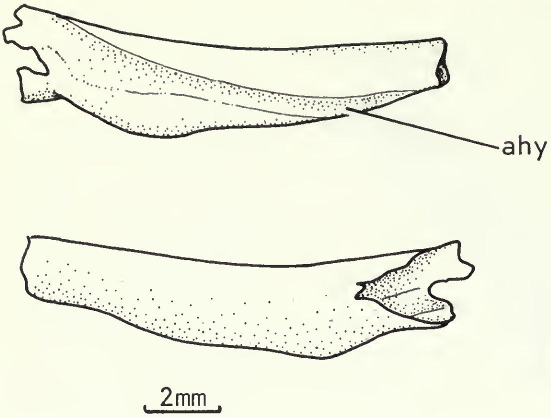

Fig. 106 *Moythomasia durgaringa* Gardiner & Bartram. Right ceratohyal in lateral (above) and medial views, from BMNH P.56475.

facet. Its medial face is slightly concave where it fitted against the lateral face of the otic region of the neurocranium, above the vestibular fontanelle and jugular canal and anterior to the exit of the vagus nerve, as in *Pteronisculus* (Nielsen 1942: fig. 47). In *Acipenser* the first suprapharyngobranchial articulates below the jugular vein, but the second articulates above it (Bertmar 1959: 305).

The second hypobranchial (Figs 111, 113) is stouter and a little longer than the first. Its distal end is broad and the articulatory facet directed dorsally. It articulated about one-third of the way along the basibranchial by a nearly vertical facet. Toothplates clothe the dorsal surface of the shank behind the expanded distal head. The second ceratobranchial is similar to the first, but epibranchial 2 is two-thirds of the length of epibranchial 1. Infrapharyngobranchial 2 is a little smaller than the first but is similarly shaped, with articular facets at either end and small toothplates ventrally. No articular facet for its anterior end has been observed on the braincase,

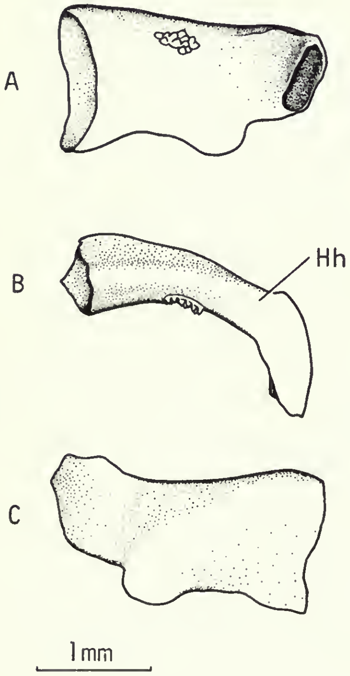

Fig. 107 *Mimia toombsi* Gardiner & Bartram. Left hypohyal in (A) medial, (B) dorsal and (C) lateral views.

but by comparison with *Acipenser* it is likely that it articulated with the ventral margin of the occiput. The second suprapharyngobranchial is a smaller version of the first. It is presumed to have articulated with (or pressed against) the occipital region, as in *Acipenser*.

The third arch has a very short hypobranchial and epibranchial and does not contain either a supra- or infrapharyngobranchial. The head of the hypobranchial is tapered and inturned where it articulated with an oblique facet on the basibranchial. Ventrally it has a process similar to that on the hypohyal, except that it lacks a perichondral covering. The third ceratobranchial is the same length and shape as the second, whereas the third epibranchial is about two-thirds the length of the second and has a characteristic broad flange projecting back from its posteromedial edge. A distinct notch in the ventral margin of this flange gives a beaked appearance to the posteroventral edge. Toothplates are confined to the lateral edge of the epibranchial.

The fourth arch, like that of *Eusthenopteron*, lacks an ossified epibranchial. This may be missing altogether, or may have been cartilaginous, as in *Latimeria*. (I erroneously attributed both a third infrapharyngobranchial and a fourth epibranchial to *Mimia*; Gardiner 1973: fig. 9). The fourth hypobranchial (Figs 111, 112) is a short, squat ossification, shorter than the third hypobranchial, which articulated by way of a broad horizontal facet with the extreme hind end of the basibranchial. The fourth ceratobranchial differs fom the third only in being somewhat shorter.

The fifth branchial arch is only represented by a ceratobranchial which is a very slender ossification, circular in cross-section and devoid of a longitudinal groove.

The basibranchial is a sturdy ossification, very similar in shape to that of *Polypterus*. The entire anterior end forms an articular facet for the hypohyals and first hypobranchials. There are three other oval facets for the remaining hypobranchials: that for hypobranchial 2 is almost vertical, that for hypobranchial 3 more oblique, and the facet for hypobranchial 4 is horizontal. The basibranchial is thickened dorsoventrally in the plane of the long axes of the facets for the second and third hypobranchials, and is also produced ventrally beneath the facets for the fourth. The dorsal surface is flat and supports a series of irregularly-arranged toothplates similar to those on the epibranchials.

Although the basibranchial is frequently a single ossification there is a clear evidence of three ossification centres in several specimens. Thus in BMNH P.53237 there are two separate ossifications with the junction between them lying behind the articulation of the third hypobranchial. The same specimen also shows a break in the perichondral covering behind the articulation facet for the second hypobranchial and this marks the junction of the first two ossification centres.

Moythomasia durgaringa

The hyomandibula of *Moythomasia* is more distinctly elbowed than that of *Mimia* and the canal for the hyomandibular trunk of the facial nerve divides as it passes obliquely down through the hyomandibula, to open by two foramina on the lateral surface of the shaft below the dermohyal. The more anterior foramen is thought to have transmitted the mandibular branch, while the posterior served for the passage of the hyoid branch (fhy.VII, Fig. 105). The remainder of the hyoid arch, the branchial arches and basibranchial agree with the corresponding structures in *Mimia*.

Hyoid and branchial arches: discussion

1. *Hyoid arch*

The hyomandibula is a clearly recognizable element in most gnathostomes and in osteichthyans where it ossifies it does so as a single bone. Most authors have agreed that it represents the epihyal in sharks (Luther 1909, Allis 1915, de Beer 1937), but some workers (Gegenbaur 1872, Holmgren 1940) have suggested that it incorporates pharyngohyal and epihyal elements; Holmgren (1943) and Jarvik (1977) proposed that in selachians, in addition to the pharyngoepihyal, there was also a ventral component from a mandibular ray. Holmgren's evidence (1940, 1943) for both selachians and actinopterygians was based on embryological

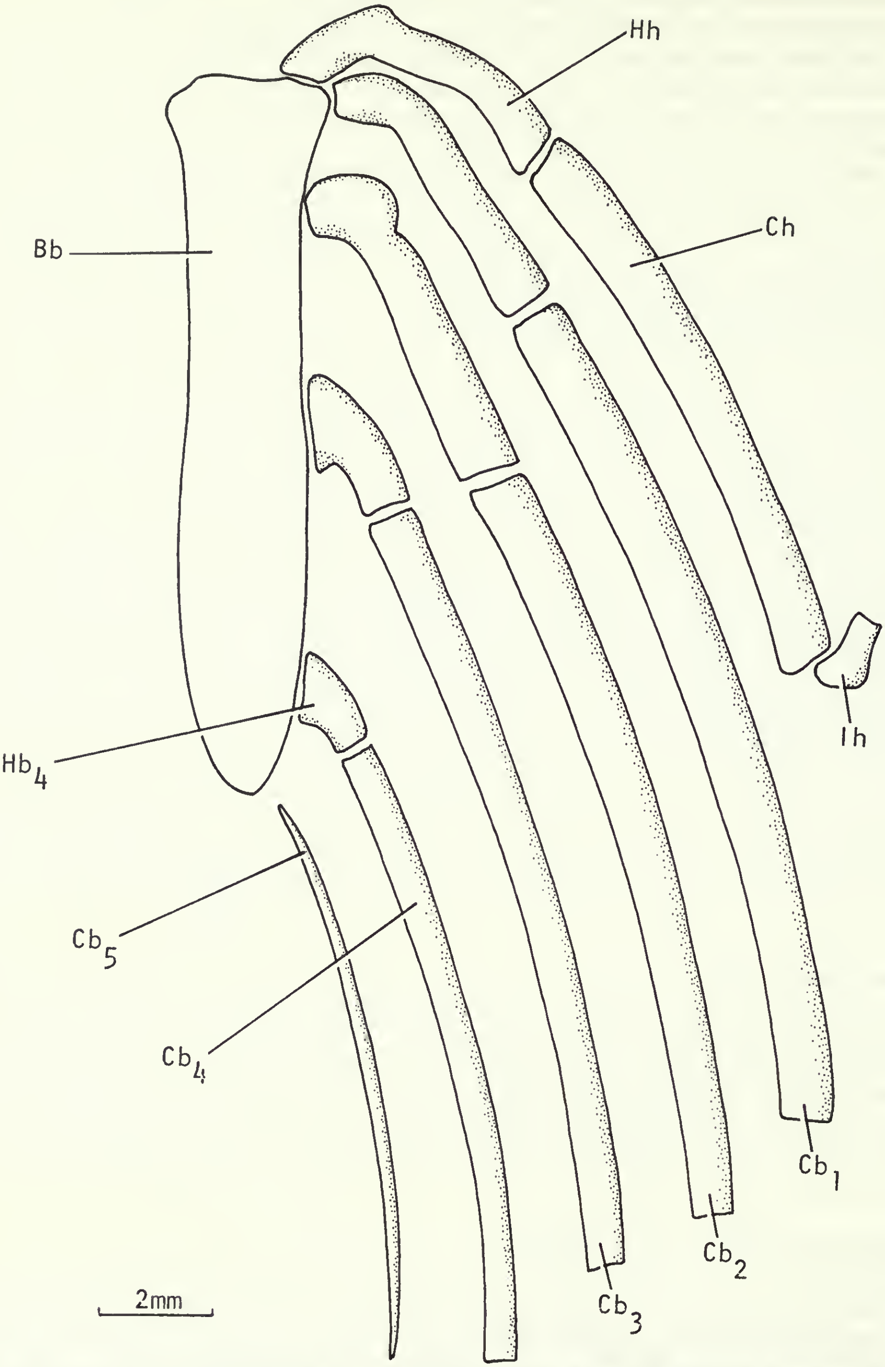
Hh
Bb
Ch
Ih
Hb4
Cb5
Cb4
Cb1
Cb2
Cb3
2mm

Fig. 108 *Mimia toombsi* Gardiner & Bartram. Restoration of ventral gill-arch elements in dorsal view. Paired elements shown on right side only.

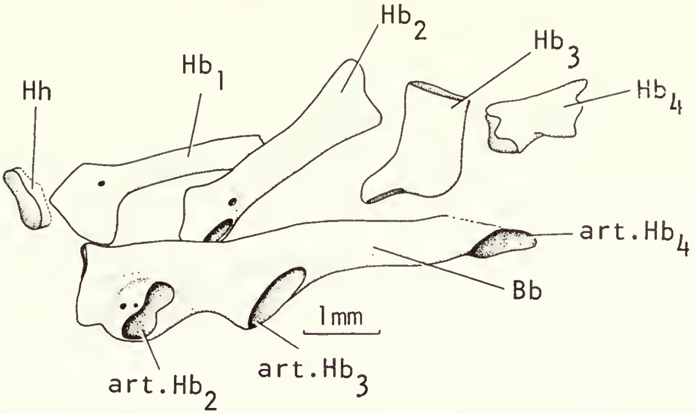
Hh
Hb1
Hb2
Hb3
Hb4
art.Hb4
Bb
1mm
art.Hb2
art.Hb3

Fig. 109 *Moythomasia durgaringa* Gardiner & Bartram. Basibranchial and hypobranchials of the right side, from BMNH P.51380.

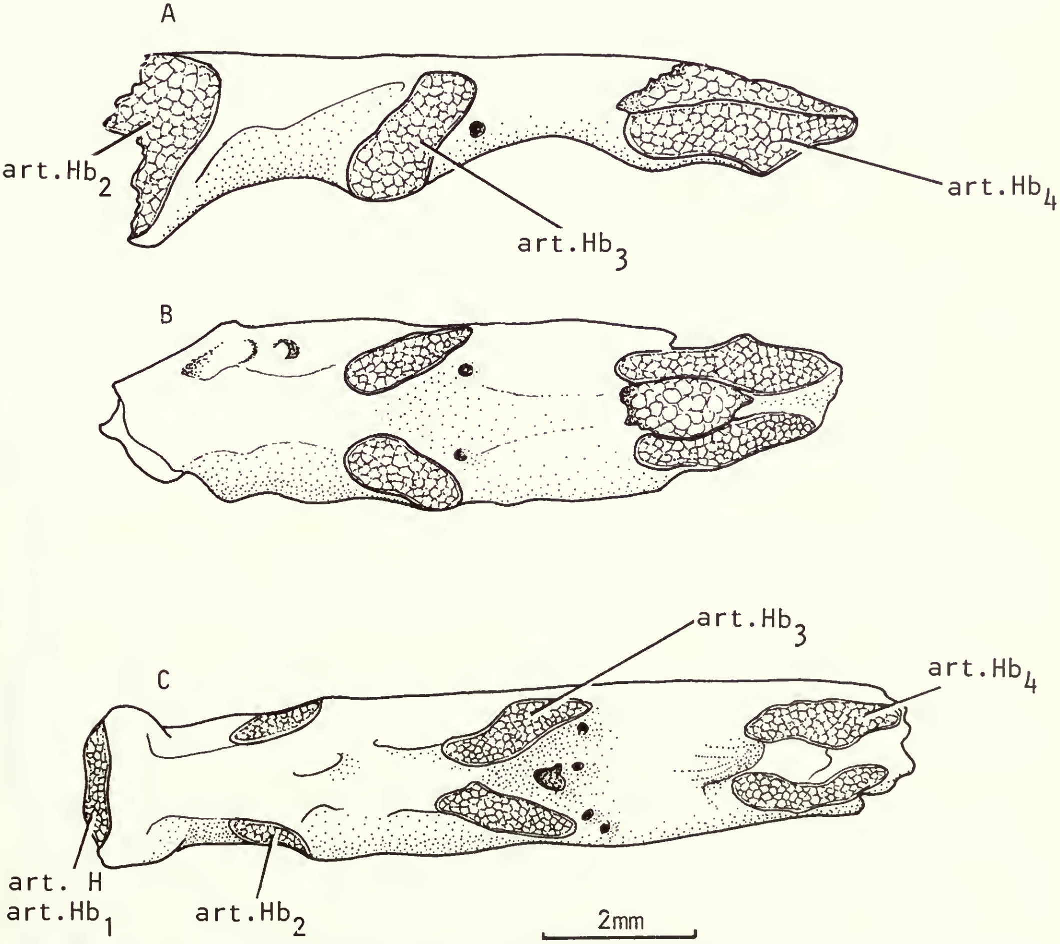
A
art.Hb2
art.Hb3
art.Hb4
B
C
art.Hb3
art.Hb4
art. H
art.Hb1
art.Hb2
2mm

Fig. 110 *Moythomasia durgaringa* Gardiner & Bartram. Basibranchial in (A), lateral and (B), ventral views, from BMNH P.53221. (C), basibranchial in ventral view from Western Australian Museum no. 20.4.244 (holotype).

stages prior to chondrification and his observed blastematic rudiments were merely mesenchymatous cell masses. Moreover his observations lead to unacceptable conclusions, such as the inference that the composition of the upper end of the hyomandibula differs in sharks and most actinopterygians from that in rays and *Acipenser*!

The presence of the interhyal in osteichthyans and of a ceratohyal ossified in two sections in neopterygians has further complicated the problem. Thus Allis (1915) believed that the hyomandibula in teleosts was essentially a pharyngohyal and the interhyal the epihyal element, while the posterior ceratohyal in neopterygians is often called an epihyal. In *Acanthodes* (Reis 1896, Miles 1964) the hyomandibula is perichondrally ossified in two sections. Miles (1964) has compared the dorsal and ventral ossifications respectively with the laterohyal and epihyal of osteichthyans, whereas Nelson (1968) regarded the dorsal element as the pharyngohyal. However, the two ossifications of the hyomandibula of *Acanthodes* are clearly in the same cartilage and this is consonant with the structure of acanthodian epibranchials which also ossify from dorsal and ventral centres (Miles 1973*a*: 93). The two ossifications of the hyomandibula of acanthodians are considered a synapomorphy of that group (compare for example the single perichondral ossification of the hyomandibula of *Jagorina, Coccosteus* and *Dicksonosteus*).

In *Neoceratodus* the cartilaginous hyomandibula is said to exhibit great variability (Ridewood 1894: 637), but if we disregard the chondrification in the hyosuspensory ligament, there are two chondrifications (Bertmar 1959, Fox 1965). The more dorsal is the hyomandibula, and the ventral the interhyal. In Devonian dipnoans these ossify separately (Miles 1977).

Finally, the hyomandibula of recent holocephalans is unique in being non-suspensory and in possessing an additional cartilage dorsally, called the pharyngohyal (Devillers 1958: 584). I consider this latter element to be a new formation and do not agree with de Beer & Moy-Thomas (1935) that the holocephalans are the only living fishes with a complete hyoid arch. A pharyngohyal is therefore regarded as an autapomorphy.

An unusual feature of the hyomandibula of *Polypterus*, many palaeoniscids and some placoderms (see p. 341) is the presence of a dermohyal. This bone, firmly bound to the dorsolateral corner, has generally been regarded as an accessory hyomandibula in actinopterygians (van Wijhe 1882, Bridge 1888) and to be serially homologous with the spiracular ossicles of *Polypterus*. Despite its obvious dermal ornamentation the dermohyal of *Polypterus* has a complex ontogenetic history. Allis (1922) said that during development it contained a piece of cartilage and he therefore regarded it as a transformed hyal ray, a view supported by Holmgren (1943) and Bertmar (1959). Holmgren (1943: fig. 45) and Daget (1950) showed that the dermohyal first appears as a perichondral bone, with Holmgren (1943: 95) adding that the subsequent bone lamella could easily be mistaken for dermal bone. I conclude that the dermohyal is a dermal element fused with the head of the hyomandibula and synapomorphous for actinopterygians and placoderms.

A peculiar feature of the hyomandibula of *Polypterus*, advanced palaeoniscids and other actinopterans is an opercular process. Although it is possible to regard the posterodorsal angle of the expanded region of the hyomandibula of *Nesides, Latimeria* and *Griphognathus*, and the posterior corner of the elbow in *Megalichthys*, as incipient opercular processes, only in actinopterygians is this process distinct. This, however, did not prevent Jarvik (1954: 32) from postulating the presence of a cartilaginous opercular process on the posteroventral margin of the hyomandibula of *Eusthenopteron*. The formation of the process itself has also caused considerable speculation; Allis (1915) for example thought it was a hyoid ray fused on to the hyomandibula, but his view was criticized by Edgeworth (1926) on the grounds that he (Allis) had not demonstrated the existence of separate cartilaginous primordia. Holmgren (1943: 86), on the other hand, maintained that the hyomandibula of *Amia* (and *Salmo*) resulted from the fusion of two blastematic rudiments, the epihyal and suprapharyngohyal (= opercular process). But these rudiments coalesce prior to chondrification and Edgeworth's criticism of Allis equally applies to Holmgren's (1940, 1943) work. In *Polypterus* the opercular process may be related to the possession of protractor hyomandibularis and dilatator opercularis muscles and in actinopterans to the dilatator opercularis. Apart from *Polypterus* an opercular process is found in *Boreosomus, Acrorhabdus, Lepisosteus* and halecostomes. An opercular process is not found

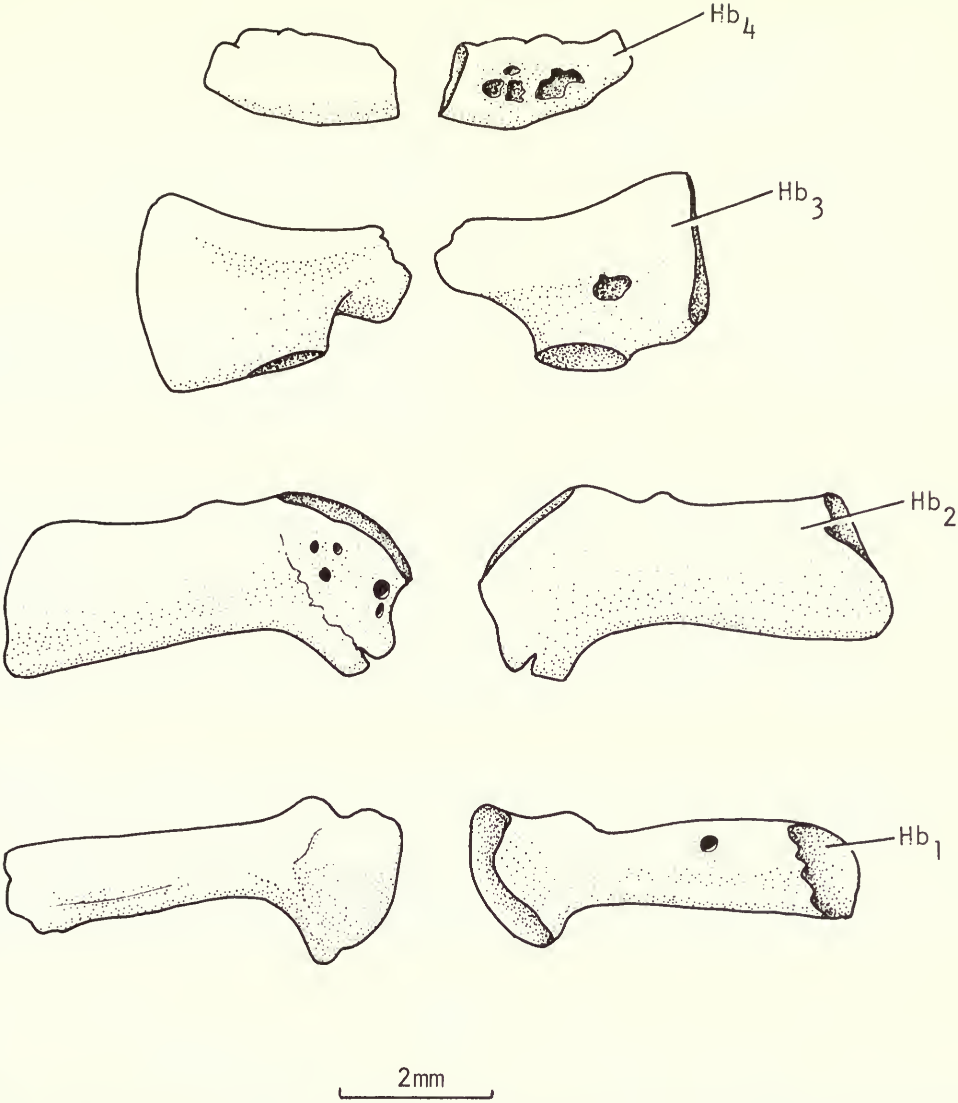

Fig. 111 *Moythomasia durgaringa* Gardiner & Bartram. Right hypobranchials in lateral (left) and medial views, from BMNH P.53256.

in *Cheirolepis, Mimia*, sturgeons and many palaeoniscids (*Elonichthys, Cheirodus*, etc.). From this evidence, and if our phylogeny is correct (Rosen *et al*. 1981, Patterson 1982), I conclude that the opercular process has arisen on at least two occasions, once in *Polypterus* and once within the actinopterans.

The hyomandibular trunk of the facial nerve passes medial to the hyomandibula in actinopterygians and turns outwards either to pass round in front of it, as in *Polypterus*, behind it as in *Acipenser* and *Polyodon*, or to penetrate the bone as in palaeoniscids and most actinopterans. In adult *Acipenser fluvescens* the hyomandibular nerve passes through a cartilaginous extension of the hyomandibula (Jollie 1980). Except in *Polypterus* the hyomandibular nerve does not divide into its mandibular and hyoid branches until it has penetrated or passed the hyomandibula. In *Polypterus* it branches prior to crossing the hyomandibula, the mandibular branch passing round the anterior face and the hyoid branch

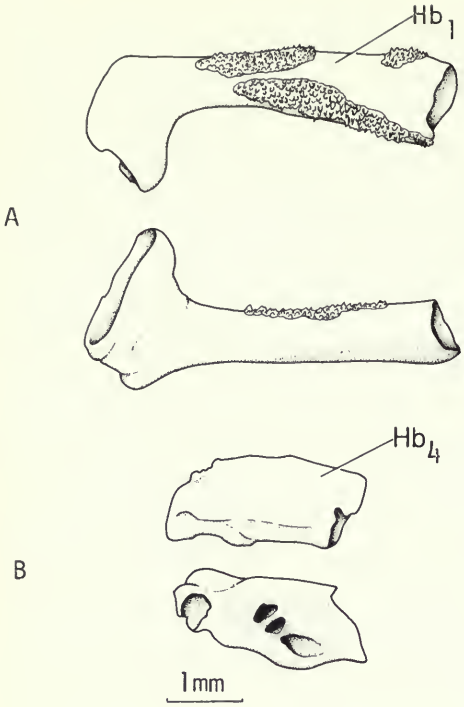

Fig. 112 *Mimia toombsi* Gardiner & Bartram. (A), right first hypobranchial in dorsal (above) and ventral views; (B), right fourth hypobranchial in dorsal (above) and lateral views; all from P.56498.

behind the posterior face, above the opercular process. The relationship of the mandibular branch in *Polypterus* is unique. In *Cheirolepis* there is no nerve foramen and the hyomandibular nerve is thought to have passed round behind the hyomandibula, as in *Acipenser*. In *Eusthenopteron, Ectosteorhachis* (Romer 1937) and *Porolepis* (Jarvik 1972) the hyomandibular nerve pierced the hyomandibula, as in most actinopterans. In *Latimeria* (Millot & Anthony 1958: fig. 20) and *Nesides* (Bjerring 1977: fig. 25) the mandibular and hyoid branches fork after

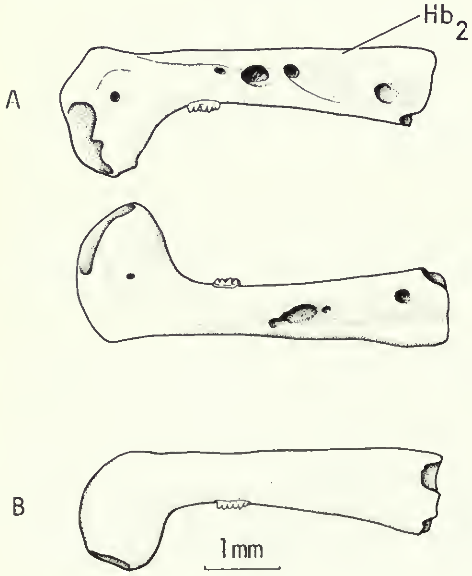

Fig. 113 *Mimia toombsi* Gardiner & Bartram. (A), second hypobranchials in ventral view; (B), right second hypobranchial in dorsal view; both from BMNH P.56498.

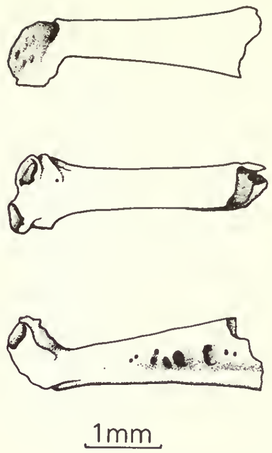

Fig. 114 *Moythomasia durgaringa* Gardiner & Bartram. Right first hypobranchial in dorsal (top), lateral (centre) and ventral (bottom) views, from BMNH P.53255.

penetrating the hyomandibula, much as in *Moythomasia*, and the hyoid branch then passes through a further small bridge of cartilage or bone before leaving the posterior margin. The hyomandibular nerve likewise passed through the hyomandibula in the fossil dipnoans *Griphognathus* and *Chirodipterus* (Miles 1977), but in *Neoceratodus* it passes anterior to it, as in selachians, before dividing into the hyoid and mandibular branches. In larval *Neoceratodus* (Bertmar 1963), in contrast, it passes through the hyomandibula.

There is no nerve foramen in the hyomandibula of placoderms (*Jagorina, Coccosteus,*

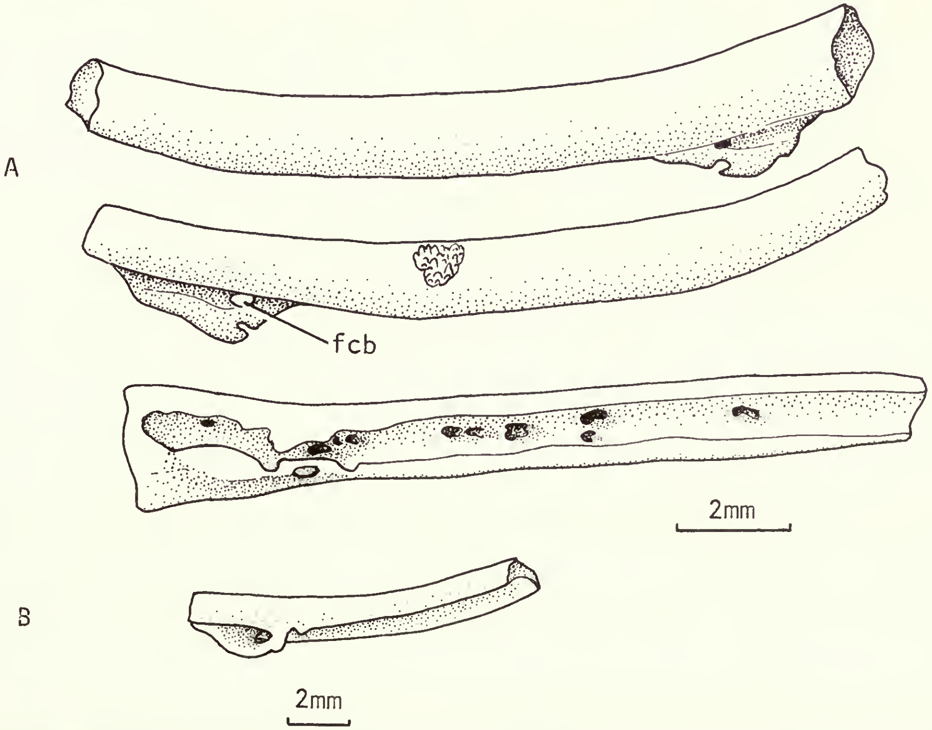

Fig. 115 *Moythomasia durgaringa* Gardiner & Bartram. (A), first left ceratobranchial in lateral, medial (centre) and ventral views, from BMNH P.53218. (B), posterior end of first right ceratobranchial in ventrolateral view, from Western Australian Museum no. 20.4.244 (holotype).

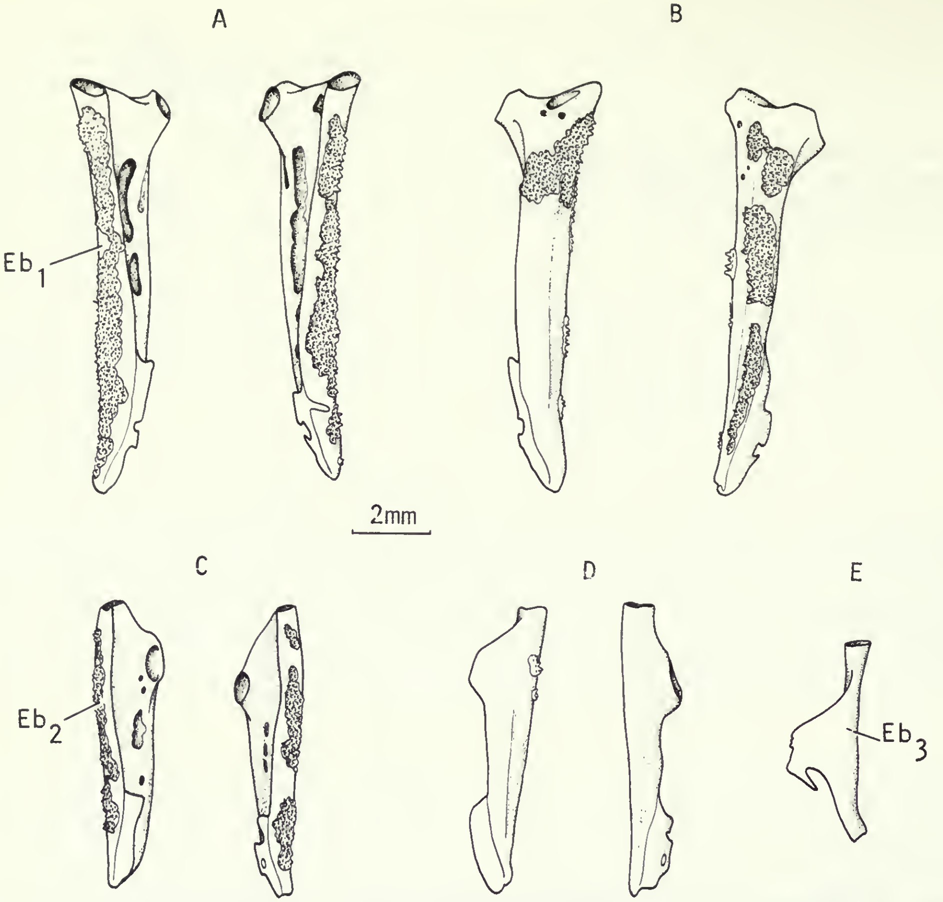

Fig. 116 *Mimia toombsi* Gardiner & Bartram. First epibranchials in (A), dorsal and (B), medial views; second epibranchials in (C), dorsal and (D), medial views; (E), third left epibranchial in lateral view. All from BMNH P.53245.

phlyctaeniids) or *Acanthodes* (Miles 1973*a*: pl. 4; Jarvik 1977: 207) and this is considered the primitive gnathostome condition.

The hyomandibula in *Mimia, Moythomasia* and *Eusthenopteron* bears a single, medial row of toothplates along its anterior margin. Jarvik (1954: 46) has homologized the toothplates of *Eusthenopteron* with the accessory hymandibula (= dermohyal) of *Polypterus*. But in *Mimia* and *Moythomasia* there are both lateral hyomandibular toothplates and a dermohyal. A medial patch of toothplates has been recorded on the hyomandibula of *Nesides* (Bjerring 1977) and *Latimeria*, and in *Elops* there is a row, much as in *Mimia*. Nybelin (1968: 441) has suggested that this series in *Elops* may be serially homologous to the medial epibranchial toothplates on the gill-arches. In *Elops* the epibranchial toothplates alternate with the gill-rakers, and both Nybelin (1968) and Nelson (1969*b*, 1970*b*) have postulated that gill-rakers are modified toothplates. Gill-rakers occur on the hyomandibula of *Acanthodes* where their presence has been taken as indicative of an open hyoid gill-slit (Watson 1937, Nelson 1968). However, Ørvig (1973: 146) and Jarvik (1977: 210) have suggested that these gill-rakers in acanthodians are endoskeletal and are therefore homologous with the cartilaginous rods which support the so-called 'gill-rakers' in sharks and dipnoans. In *Acanthodes* the hyomandibular gill-rakers form a single series which projects ventromedially into the pharynx (Miles 1973*a*). A similar single series of hyomandibular gill-rakers has been recorded in the selachian *Cetorhinus*, the

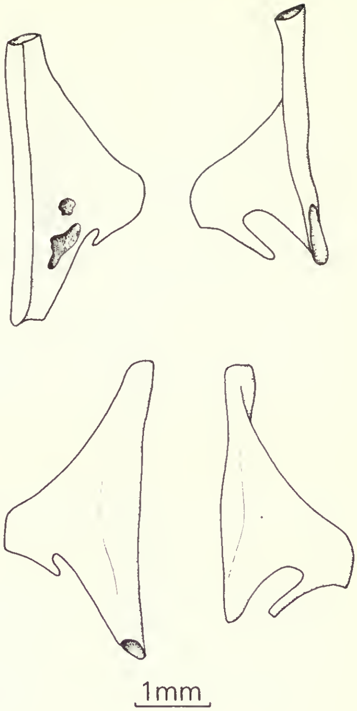

Fig. 117 *Mimia toombsi* Gardiner & Bartram. Third epibranchials in dorsal (above) and ventromedial views, from P.56474.

holocephalan *Callorhynchus* and the teleost *Neonesthes* (Holmgren 1942, Miles 1973*a*). There is therefore no need to invoke the aphetohyoid hypothesis to explain their occurrence in acanthodians. Whether or not hyomandibular gill-rakers are a primitive gnathostome feature is uncertain; from their distribution within the phylogeny they appear to have arisen on more than one occasion.

The remainder of the hyoid arch may consist of one further cartilage (= ceratohyal) as in chondrichthyans, or several as in osteichthyans.

In osteichthyan fishes there is invariably a separate ossification or cartilage linking the hyomandibula with the ceratohyal, the interhyal, and this is considered synapomorphous for the group. In Recent chondrosteans the cartilage is hypertrophied and has often been incorrectly referred to as a symplectic (Gardiner 1973, Patterson 1982). An accessory element between the hyomandibula and the ceratohyal has been described in one specimen of *Acanthodes* (Miles 1973*a*: fig. 15; pl. 7) but the evidence is equivocal (see BMNH P.4990).

In osteichthyans there is a further separate ossification or cartilage in front of the ceratohyal, the hypohyal. This, like the interhyal, is synapomorphous for that group. In teleosts other than pholidophorids and some osteoglossomorphs the hypohyal contains two ossifications (Patterson 1982).

The single ventral hyoid cartilage (called ceratohyal) of chondrichthyans is matched in acanthodians. In *Acanthodes* (Fig. 120) it is perichondrally ossified in two sections (one at either end), like the hyomandibula, epibranchials and ceratobranchials (Miles 1973*a*). This has allowed the anterior ossification to be mistaken for a hypohyal (Watson 1937: fig. 18A; Nelson 1968: fig. 3A, B), but in presumed mature individuals of *Acanthodes* the ceratohyal is all one ossification (BMNH P.49977). It is therefore simpler to regard this mode of ossification as synapomorphous for acanthodians.

In many osteichthyans there is either a single ceratohyal ossification (*Cheirolepis, Mimia, Polypterus, Glyptolepis, Latimeria*) or a single cartilage (*Neoceratodus, Necturus*). In neopterygians (*Pteronisculus, Lepisosteus, Amia*, teleosts), however, the ceratohyal is ossified

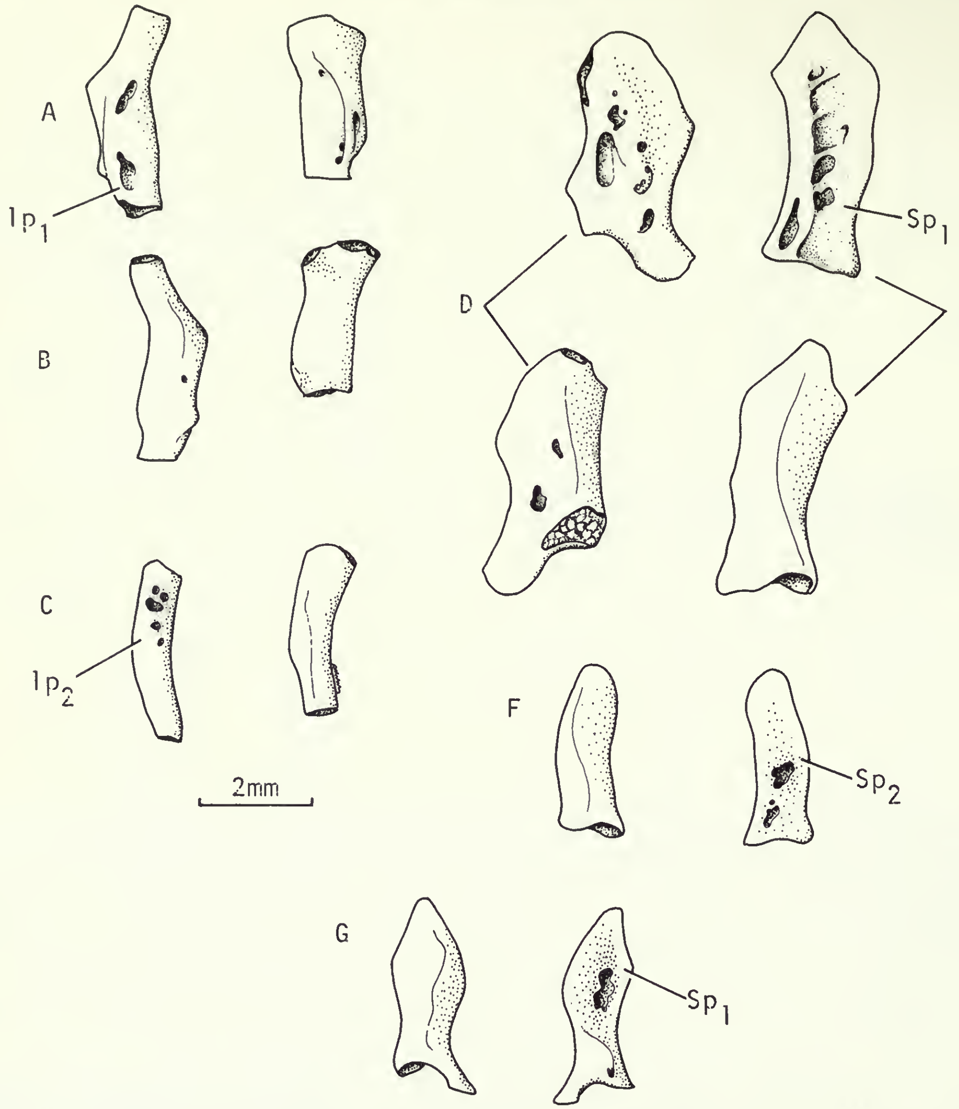

Fig. 118 Infrapharyngobranchials and suprapharyngobranchials. A–C, E, G, *Mimia toombsi* Gardiner & Bartram. (A) first infrapharyngobranchials in dorsal and (B) ventral views; (C) second left infrapharyngobranchial in dorsal view, second right in ventral view; (E) first right suprapharyngobranchial in medial (top) and lateral views; all from P.53245. (G) second left suprapharyngobranchial in lateral (left) and medial views, from BMNH P.56474. D, F, *Moythomasia durgaringa* Gardiner & Bartram. (D) first right suprapharyngobranchial in medial (top) and lateral views; (F) second right suprapharyngobranchial in lateral (left) and medial views; both from BMNH P.53256.

in two sections which parallel those in *Acanthodes*, while in recent chondrosteans there are two separate cartilages (ceratohyal and interhyal of previous authors, but see Patterson 1982). The posterior ceratohyal cartilage in *Polyodon* carries a branchiostegal ray, as does the posterior ceratohyal in *Lepisosteus*. Two ceratohyal cartilages are considered to be an unique feature of chondrosteans and two ceratohyal ossifications a synapomorphy of neopterygians, where they always remain separate and do not fuse as they do in acanthodians.

The remaining element in the hyoid arch is the symplectic. There are three kinds of symplectic recorded in fishes (Gardiner 1973, Patterson 1973, 1982); that in Recent chondrosteans, which is probably a hypertrophied interhyal, that in neopterygians, which is confluent with the hyomandibula, and that in actinistians. The neopterygian symplectic develops as an anteroventral outgrowth of the hyomandibular cartilage which ossifies independently. It therefore remains intimately attached to the hyomandibula and is applied to the quadrate in teleosts or to the quadrate and lower jaw in halecomorphs (Patterson 1982). This type of symplectic is considered synapomorphous for neopterygians (Patterson 1973: 262).

In *Latimeria* the symplectic is a large, partly ossified, independent cartilage which is connected by a ligament to the hyomandibula. It articulates with the interhyal and ceratohyal dorsally and with the lower jaw ventrally. The articulation with the lower jaw is posterior to and separate from that between the quadrate and lower jaw. These articulations are therefore in tandem (Forey 1981) and not side by side as in halecomorphs. Like Forey (1981), I consider this tandem double jaw articulation synapomorphous for actinistians, and like Patterson (1982) I regard the actinistian symplectic as characteristic of that group and non-homologous with the neopterygian symplectic.

2. *Basibranchial and branchial arches*

Normally in gnathostome fishes there is a series of five arches (Nelson 1969*b*). Dorsally they consist of paired epi- and pharyngobranchials and ventrally of paired hypo- and ceratobranchials.

There are hypobranchials in the first four arches in many osteichthyans, though in *Acipenser* and most teleosts (Patterson 1977*a*) only the first three are developed. Four hypobranchials are also present in most chondrichthyans, and this is believed to be the condition in acanthodians (Nelson 1968, Miles 1973*a*). However, the structures which Miles (1973*a*) identified as hypobranchials in *Acanthodes* have been alternatively interpreted as basibranchials by Rosen *et al.* (1981), and in turn the hypobranchials of Watson (1937) and Nelson (1968, 1969*b*) have been interpreted as anterior ceratobranchials by Miles (1973*a*). Re-examination of Watson's and Miles' material has persuaded me that the ceratobranchials are perichondrally ossified in two portions and that the ossifications lying anterior to the second, third and fourth are hypobranchials (Miles 1973*a*: fig. 18, hy.br 2–4) and not basibranchials as Rosen *et al.* (1981) presumed. The ossifications in question are inturned anteriorly and a single basibranchial (Fig. 120) against which the ceratohyal and first ceratobranchial articulated can be seen in several specimens (e.g. BMNH P.49977; Miles 1973*a*: pl. 5B, b.br). Often, only the anterior end of the

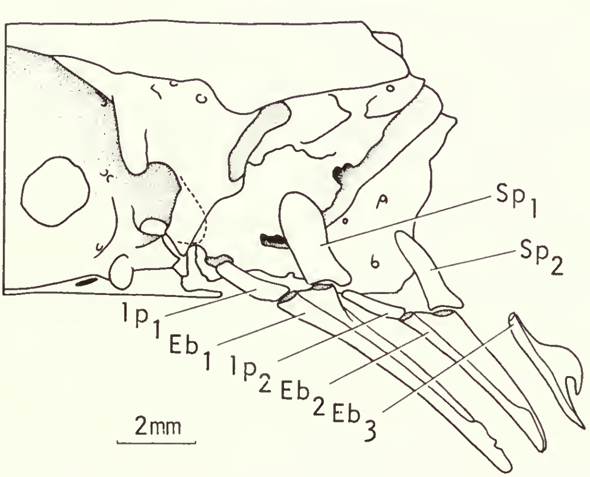

Fig. 119 *Mimia toombsi* Gardiner & Bartram. Reconstruction of posterior part of the neurocranium and dorsal gill-arch elements in lateral view.

basibranchial is ossified (basihyal of Watson 1937, and see BMNH P.49933, P.44934). There is no hypobranchial in the first arch in *Acanthodes*.

The basibranchial in chondrichthyans usually consists of two large, distinctly separated cartilages or copulae, but subdivision of these may occur, particularly in holocephalans. The ceratohyal and first branchial arch often articulate with the anterior cartilage (*Heterodontus, Heptanchus, Squatina*) and the first arch slants obliquely forwards and downwards. The succeeding hypobranchials point backwards to meet the anterior border of the posterior cartilage, and this is considered synapomorphous for chondrichthyans.

In actinopterygians a single basibranchial ossification has been reported in *Polypterus, Mimia* and *Moythomasia*. In the Gogo palaeoniscids the basibranchial is composed of three ossification centres which presumably fused during ontogeny, and which were obviously in the same cartilage. They correspond to the three basibranchials of *Pteronisculus* and *Birgeria* and to the three minute ossifications recorded in the cartilaginous basibranchial of *Acipenser* by van Wijhe (1882). In *Polyodon* and teleosts there are three separate cartilages, but in *Lepisosteus* and *Amia* there are four. The first three copulae in *Lepisosteus* and the second in *Amia* are perichondrally ossified. The segmentation seen in the basibranchials of *Amia* and *Lepisosteus* must have occurred independently in each form and four copulae cannot be regarded as synapomorphous for neopterygians (cf. Wiley 1976). The basibranchial in *Polypterus* comprises a single ossification which possibly corresponds to the first or anterior ossification in *Mimia* and *Pteronisculus* (Patterson 1982).

Elsewhere in osteichthyans a basibranchial consisting of more than one ossification has been described only in *Eusthenopteron* (Jarvik 1954). The division between the two ossifications is in exactly the same position as that between the two anterior ossifications of *Mimia*. Whether these two ossifications are in a single cartilage, as in *Acipenser* and *Mimia*, or represent separate cartilages, as in *Polyodon*, we have no means of knowing.

In *Latimeria, Glyptolepis* and *Laccognathus* the copula resembles a greatly foreshortened *Polypterus* basibranchial. The basibranchial of *Neoceratodus* and larval urodeles is similar though considerably reduced. A small, triangular basibranchial has also been described in the Devonian dipnoans *Griphognathus* and *Chirodipterus*. However, Miles (1977) has suggested that the basihyal in these fossils is in fact a co-ossified anterior basibranchial and basihyal and accordingly restored the bases of the first two arches on this ossification. Rosen *et al.* (1981) suggest that if all the arches were restored entirely on the triangular basibranchial then the arrangement of the gill-arch bases would be similar to *Neoceratodus*. Since cartilages rarely fuse during development (although they may divide), and a separate cartilaginous basihyal is present in *Neoceratodus*, I abide by our solution (Rosen *et al.* 1981) and thus a single broad, triangular basibranchial is a synapomorphy of porolepiforms, actinistians and dipnoans (non-homologous with that of *Polypterus*). Other gill-arch synapomorphies of that group include the reduction or loss of hypobranchials in actinistians, dipnoans and larval urodeles and the articulation of the last gill-arch with the base of the preceding arch in porolepiforms, actinisitians, dipnoans and larval urodeles (Rosen *et al.* 1981). I further conclude that the primitive osteichthyan possessed a single, cartilaginous basibranchial with at least two ossification centres. A similar basibranchial may have been present in acanthodians (see Fig. 120). In acanthodians and chondrichthyans the hyoid and first gill-arch articulate with the anterior basibranchial and in osteichthyans at least the second gill-arch also articulates with it. This latter condition is synapomorphous for osteichthyans (Rosen *et al.* 1981).

Anterior to the basibranchial a further ossification occurs in advanced actinopterans, *Eusthenopteron* and dipnoans. It is usually referred to as the basihyal (Nelson 1969*b*), though Jarvik (1954) regarded it as a member of the sub-branchial series and accordingly referred to it as the 'sublingual rod'. A cartilaginous basihyal is also found in larval apodans, lizards and *Sphenodon* (de Beer 1937). This should not be confused with the paired processus lingualis of chelonians and birds (also called paraglossum or entoglossum), which appears to be homologous with the anterior horns (or hyoid arch or lesser cornu) of *Echidna* (Goodrich 1930: fig. 474). The basihyal in actinopterans is confined to teleosts where it occurs in

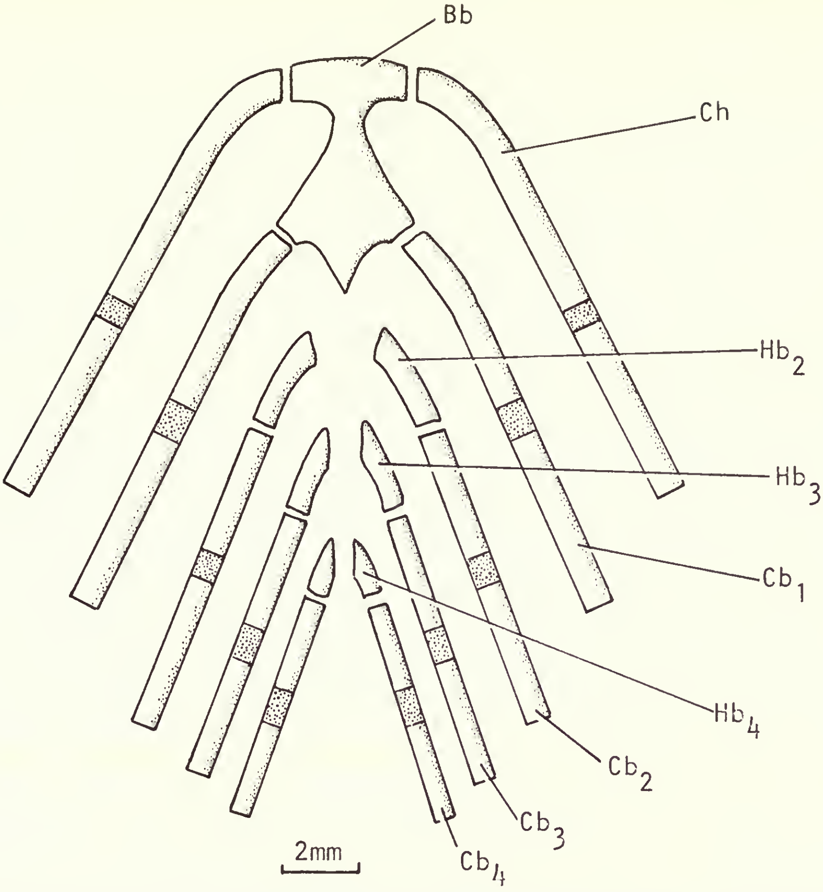

Fig. 120 *Acanthodes bronni* Agassiz. Reconstruction of ventral part of gill-arch skeleton in dorsal view. Based on BMNH specimens.

osteoglossomorphs and those cladistically more derived groups (Patterson 1977*a*). It appears to chondrify separately from the basibranchial in *Salmo* (de Beer 1937) and *Gasterosteus* (Swinnerton 1902), and usually supports a median dermal toothplate which may bear large teeth. The basihyal of *Eusthenopteron* is a long, narrow bone with a strong median ridge dorsally (Jarvik 1954). A similarly-enlarged basihyal is present in *Griphognathus* where it supports two pairs of toothplates. In *Conchopoma* there is a single, median toothplate. Miles (1977: 286) has suggested that the elongation of the basihyal in *Griphognathus* may be correlated with secondary elongation of the lower jaw (the basihyal cartilage in *Neoceratodus* remains small) and that the similar basihyals in *Eusthenopteron* and *Griphognathus* are the result of parallel evolution. The absence of basihyals in actinistians, porolepiforms and primitive actinopterygians and the lack of other plausible synapomorphies between *Eusthenopteron* and dipnoans (Rosen *et al.* 1981) suggest that the basihyal has arisen on at least three occasions (teleosts, *Eusthenopteron*, dipnoans and tetrapods).

Associated with the dorsal surface of the basibranchial is a series of toothplates. Nelson (1969*b*) hypothesized that the plesiomorphous gill-arch dentition of osteichthyans consisted of six rows of dermal elements, and that paired basibranchial toothplates were primitive for osteichthyans. Paired basibranchial toothplates are found in fossil actinistians where they are arranged in three pairs lying opposite the first three gill-arches (Forey 1981). In *Latimeria* the toothplates are insignificant and according to Nelson (1969*b*) are an adventitious formation. If Forey's (1981) phylogeny of the actinistians is correct this would seem to be the most parsimonious hypothesis. In *Eusthenopteron* (Jarvik 1954) there are two pairs of toothplates on each basibranchial, and also a lateral row of smaller plates related to the hypobranchials. In *Mimia* and *Moythomasia* there are numerous, irregularly-arranged small toothplates over the whole dorsal surface of the basibranchials and in *Polypterus* two widely-separated rows of asymmetrical plates which come together posteriorly. In *Acipenser* (Jollie 1980) two transverse bands of teeth cross the copula at the level of hypobranchials 1 and 2. In *Bobasatrania, Errolichthys* and in teleosts other than Pachycormiformes a median toothplate covers the basibranchials. These observations suggest that primitively the osteichthyan basibranchial was covered by numerous toothplates which have been aligned into four rows in *Eusthenopteron*, and into two rows in actinistians (and *Griphognathus*). There is a median plate in teleosts (and *Conchopoma*).

Situated beneath the basibranchial and joined anteriorly by ligaments to the hypohyals is a median bone, the urohyal (in *Polypterus* the ligaments are ossified). In actinopterygians a urohyal occurs in *Polypterus, Australosomus* (Patterson 1977*b*) and teleosts. In *Australosomus* and pholidophorids it is presumed to ossify in cartilage bone, but in *Polypterus* and extant teleosts it ossifies in membrane bone. Patterson (1977*b*) has convincingly demonstrated the dual nature of the teleostean urohyal and has hypothesized that it represents the fused interclavicle and urohyal, the interclavicle having sunk beneath the surface. Interestingly the interclavicle has also sunk beneath the surface in many actinistians (Forey 1981). An endochondral urohyal also occurs in Devonian and Carboniferous actinistians, *Latimeria*, porolepiforms, osteolepiforms (Jarvik 1963), Devonian dipnoans (Miles 1977), urodeles and anurans (Jarvik 1963, Patterson 1977*b*). The urohyal is presumed to have remained cartilaginous in the Gogo palaeoniscids and *Pteronisculus*. The presence of a urohyal is therefore hypothesized as plesiomorphous for osteichthyans.

Turning to the dorsal parts of the arches we find that in some actinopterygians and sarcopterygians there are two types of pharyngobranchials, infra- and suprapharyngobranchials. The presence of the latter has been regarded as a synapomorphy of osteichthyans by Rosen *et al.* (1981).

Allis (1925) and Holmgren (1942) suggested, mainly on evidence of orientation, that the osteichthyan suprapharyngobranchial was homologous with the chondrichthyan pharyngobranchial. By contrast Nelson (1968) homologized the infrapharyngobranchial with the chondrichthyan (and acanthodian) pharyngobranchial because in both groups they support the pharyngeal roof and denticles. Nelson (1968) also suggested that the condition in the first arch of *Eusthenopteron*, where there is a presumed compound supra-infrapharyngobranchial, could be primitive for osteichthyans and might be the equivalent of the pharyngobranchial of *Acanthodes*. He further imagined that the dorsal process of an *Acanthodes* pharyngobranchial might be the homologue of the suprapharyngobranchial. Miles' (1973*a*: fig. 16) redescription of the pharyngobranchials of *Acanthodes* has firmly persuaded me of the efficacy of Nelson's (1968) hypothesis that the form of the pharyngobranchials of *Acanthodes* is primitive for gnathostomes. Thus I believe that the acanthodian pharyngobranchial is homologous with that of chondrichthyans and both the infra- and suprapharyngobranchials of the anterior arches of osteichthyans and with the pharyngobranchial of the third arch in actinopterygians.

In *Latimeria*, where the first pharyngobranchial is a single, slender, dorsally-directed rod, both Millot & Anthony (1958) and Nelson (1968) have interpreted it in the light of *Eusthenopteron* and considered it to represent a compound supra-infrapharyngobranchial. But this rod appears serially homologous with the second suprapharyngobranchial, and furthermore the contact between the first infrapharyngobranchial and the braincase seen in primitive actinopterygians and *Eusthenopteron* is replaced in *Rhabdoderma* by a direct contact between the first epibranchial and the braincase (Forey 1981). Both the first and second epibranchials contact the braincase in *Latimeria*. An analogous articulation occurs between the first epibranchial and the auditory capsule in *Polypterus*, but here the infrapharyngobranchial remains and articulates in the angle of the parasphenoid, as in *Amia* and some teleosts. In most teleosts the infrapharyngobranchial articulates with the parasphenoid rather than with the prootic (Patterson & Rosen 1977: 129).

Suprapharyngobranchials occur in several actinopterygians, including *Mimia, Moythomasia, Polyodon, Acipenser, Pteronisculus, Australosomus, Lepisosteus* and teleostean fishes of the families Elopidae and Alepocephalidae (Nelson 1969*b*); in actinistians (*Latimeria*) and in *Eusthenopteron*. Usually they are two in number. Their absence from the first arch in *Polypterus* is considered derived and related to the contact between the first epibranchial and auditory capsule. Infrapharyngobranchials occur on the first three arches in many actinopterans, including *Pteronisculus, Australosomus, Acipenser, Lepisosteus* and *Amia*, though it is possible to regard this third infrapharyngobranchial as an undifferentiated pharyngobranchial. There are only two infrapharyngobranchials in *Eusthenopteron* and *Mimia* and one in *Latimeria* (2nd) and *Polypterus* (1st). In Recent teleosts there are four pharyngobranchials.

From this survey I hypothesize that the primitive osteichthyan possess two suprapharyngobranchials (on the first two arches) and that three, not four, pharyngobranchials is plesiomorphic for osteichthyans (cf. Nelson 1969*b*). Furthermore, the loss of pharyngobranchials (including infra- and supra-) is a synapomorphy of choanates (Rosen *et al.* 1981).

There are usually four pharyngobranchials in chondrichthyans and four have also been inferred in acanthodians (Nelson 1968, 1969*b*). However, careful examination of the numerous casts of *Acanthodes* made by Dr Roger Miles of material from the Humboldt University, Berlin, the Palaeontological Institute of the University of Bonn and the University Museum of Zoology, Cambridge, failed to reveal more than three pharyngobranchials. Despite some controversy (Miles 1964, 1965, Nelson 1968, 1969*b*) it is now generally agreed that the pharyngobranchials of *Acanthodes* projected posteromedially into the roof of the pharynx (Miles 1973*a*). Thus the posterior position of the gill-arches and the posterior orientation of the pharyngobranchials in chondrichthyans and acanthodians are considered to be shared primitive characters.

Axial skeleton

Mimia toombsi

The axial skeleton is represented by dorsal and ventral arcual elements throughout its length and by supraneurals and ribs in the abdominal region. The individual ossifications are perichondral shells. The notochord was persistent and there is no trace of centra.

The dorsal arcual ossifications are always paired and are presumed to be basidorsals. No separate interdorsals have been observed and in this respect *Mimia* resembles *Polypterus, Lepisosteus*, teleosts etc. (Gardiner 1983). In the abdominal region each basidorsal ossification (na, Figs 121, 123) consists of a proximal plate or neural arch and a long distal process or neural spine. On the lateral face of the neural arch there is a well-developed, laterally-directed epineural process (epi, Fig. 121). Similar processes in the diapophysial position are found on the anterior vertebrae of *Australosomus, Boreosomus* (Nielsen 1949: figs 41, 42, 47, 48), *Caturus* (Gardiner 1960: fig. 33, Patterson 1973: 237) pholidophorids, *Elops* etc. and the dipnoan *Griphognathus* (Rosen *et al.* 1981: fig. 54A). These epineural processes are found on each of the first 14 vertebrae in *Mimia*. That on the first is very stout and terminates in several finger-like projections (Fig. 121D). The bases of all the epineural processes are perforated or notched for the passage of the intersegmental artery. The second basidorsal of *Boreosomus* (Nielsen 1949: fig. 48) likewise has a foramen in its epineural process. The medial faces of the neural arches are devoid of perichondral lining where they embraced the spinal cord. Posterior to the dorsal fin the neural spines decrease in length caudally and towards the end of the tail some of the basidorsals are incompletely segmented from one another and the junction between them is marked by foramina for the spinal nerves. This is particularly marked in *Moythomasia* (BMNH P.53255).

Above the basidorsals of the abdominal region there is a series of unpaired supraneurals. This series terminates a short distance in front of the dorsal fin (Fig. 124).

The ventral arcual elements are unpaired and are presumed to represent basiventrals. In the abdominal region these elements are semicircular in cross section with a posteriorly-directed

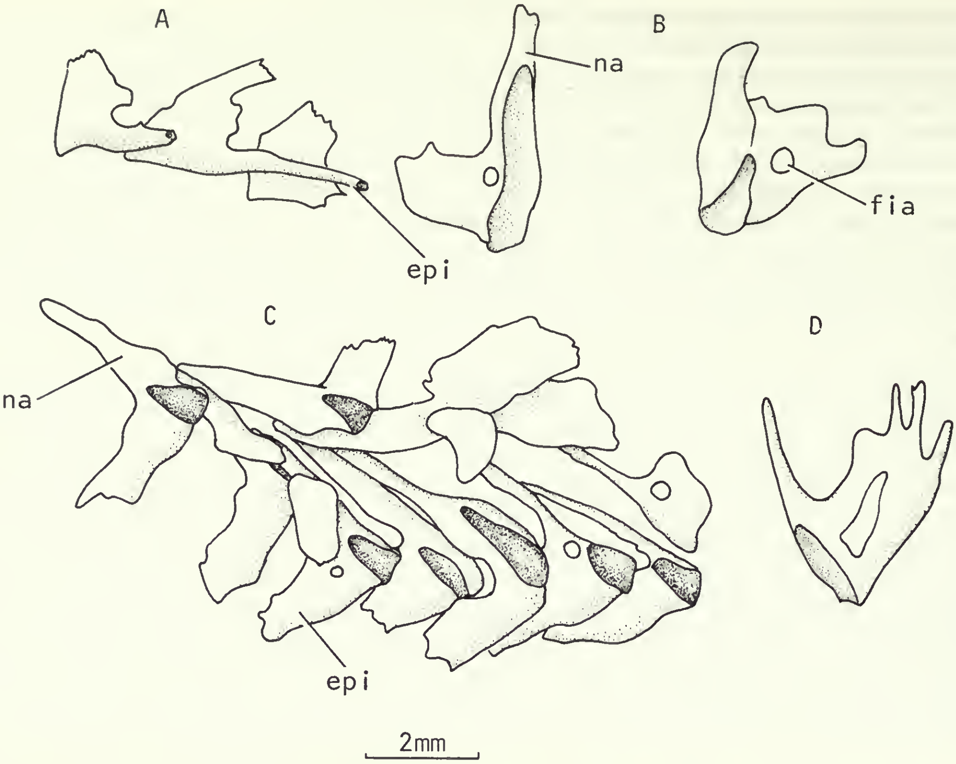

Fig. 121 *Mimia toombsi* Gardiner & Bartram. Neural arches and spines from anterior part of vertebral column in (A) lateral and (B), (C), (D) anteromedial views. (A) from Western Australian Museum no. 70.4.245 (holotype), (B) from BMNH P.56500, (C) and (D) from BMNH P.53228.

median keel similar to that in *Pteronisculus* (Nielsen 1942: fig. 49). Ossified ribs articulated with the lateral face of the abdominal basiventrals. In the region of the anal fin the ventral arcual elements or haemal arches have well-developed median haemal spines (ha, Fig. 122A, B, C, D, E, G) whose bases enclose the aortic or haemal canal. The lateral faces of the haemal arches in this region are perforated by foramina for the intersegmental arteries (fia, Fig. 122C), as in *Caturus* (Rosen *et al.* 1981: fig. 59A, B). Occasionally the roof of the haemal canal may also have a median perforation (Fig. 122E).

In the caudal region there is a series of 22 stout hypurals which decrease in length posteriorly (Fig. 124). The caudal lepidotrichia embrace the ends of these hypurals.

Moythomasia durgaringa

In several specimens remnants of the axial skeleton are visible and these appear to be identical with those of *Mimia*. However, in the caudal region the neural arches and their spines are fused and the neural spine is median, as in the caudal region of *Birgeria*.

Axial skeleton: discussion

1. *Arcualia*

Four pairs of arcualia were primitively present in each segment of gnathostomes (Gardiner 1983), and in all osteichthyans they are represented by ossified or cartilaginous elements in at least part of the vertebral column. In actinopterygians they occur throughout the whole column in *Acipenser* and *Polyodon*, in *Pteronisculus* they are restricted to the abdominal region and in *Australosomus, Caturus* and *Pholidophorus* to the caudal region. Separate interdorsals and

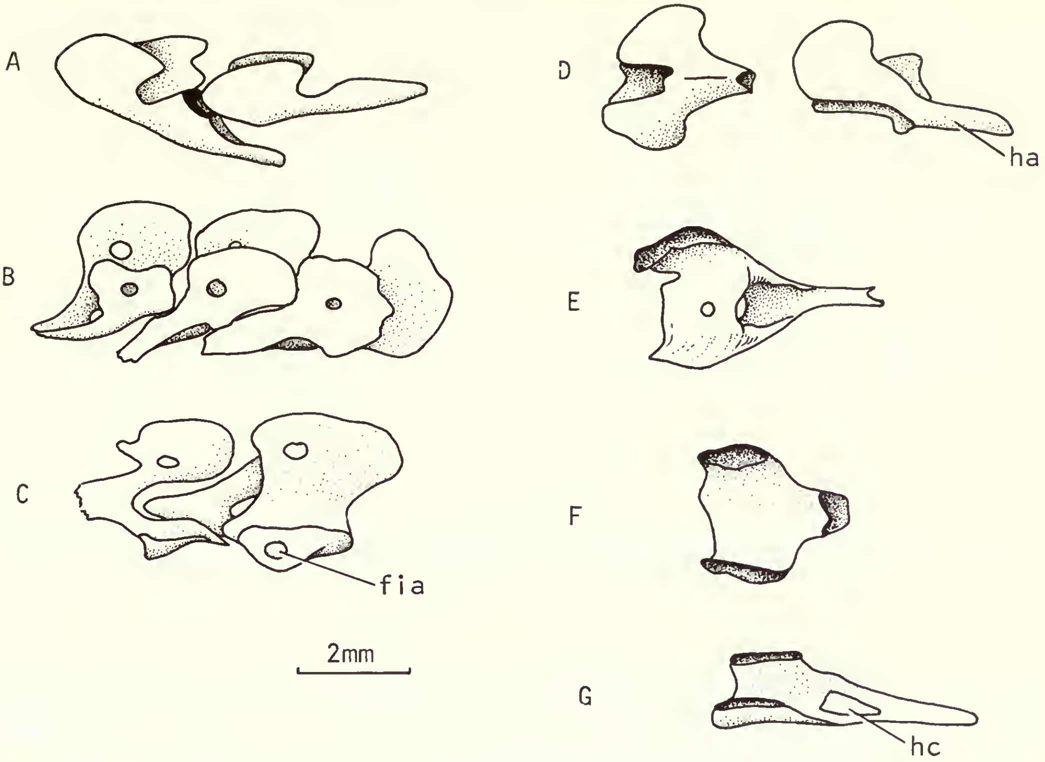

Fig. 122 *Mimia toombsi* Gardiner & Bartram. Haemal arches from the anterior part of the caudal region in (A), (B) lateral, (C(, (G) dorsolateral, (E), (F) dorsal, and (D) ventral views. (A), (B), (C) from Western Australian Museum no. 70.2.245 (holotype), (D) from BMNH P.53232, (E) from BMNH P.56494, (F) and (G) from BMNH P.56500.

interventrals are missing in *Polypterus* and *Lepisosteus*, and from the development of most teleosts; separate interventrals are missing from the trunk of developing *Amia*.

In actinistians (*Latimeria*) the full complement of arcualia is confined to the caudal region; in *Neoceratodus* the two dorsal pairs are present only in the caudal area whereas the two ventral pairs are only found in the anterior trunk. In *Eusthenopteron, Osteolepis, Glyptolepis* and most temnospondyls the two dorsal pairs are always present although ventrally there is only a single element. However, as in *Latimeria*, the full complement is seen in the tail region of several tetrapods (*Archegosaurus, Chelydosaurus*).

2. *Centra*

The earliest recorded actinopterygian centra are the thin, ring centra of *Haplolepis* (Baum & Lund 1974) from the Upper Carboniferous. These ring centra comprise thin calcifications in the notochordal sheath and are developed from dorsal and ventral hemicentra. Similar ring centra occur in the tail of *Pygopterus*, but in *Turseodus* there are separate dorsal and ventral hemicentra.

Chordacentra appear to have been independently acquired in the pholidopleurids, and in *Australosomus* (Nielsen 1949) they are overlain by endochondrally ossified neural and haemal arches and interdorsals. By the end of the Jurassic many actinopterygians possessed calcifications in the notochordal sheath including hemichordacentra in *Furo philpotae* (Agassiz) and *Caturus* and complete chordacentra in pholidophorids, archaeomaenids, some pachycormids, pleuropholids, catervariolids, *Galkinia* and *Ichthyokentema* (Patterson 1973). Today the notochordal sheath is still involved in the early ontogenetic stages of centrum formation in

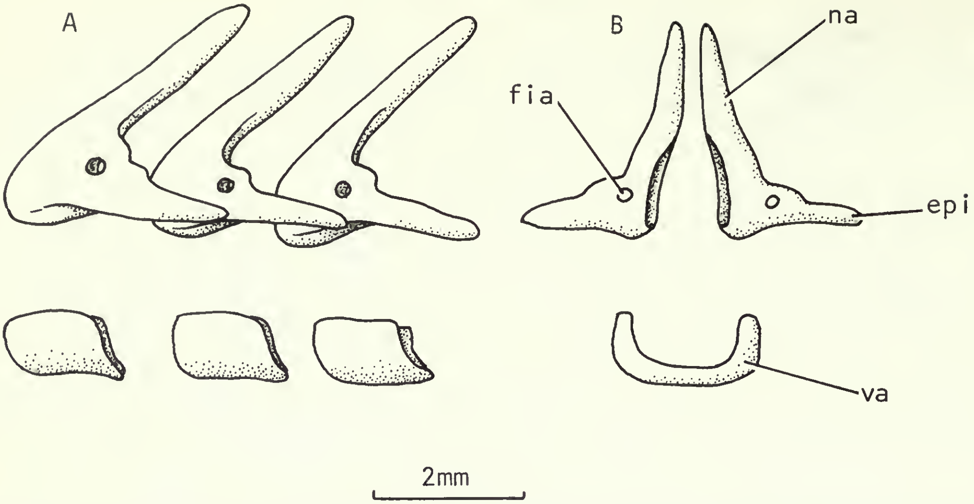

Fig. 123 *Mimia toombsi* Gardiner & Bartram. Restoration of part of the vertebral column from the anterior abdominal region: (a), lateral view, (b), anterior view.

primitive living teleosts and if our phylogenies are correct (Patterson 1973, 1977*a*, Rosen *et al.* 1981) then chordacentra must have arisen on at least three occasions within the actinopterygians (haplolepids, pholidopleurids and halecostomes).

By the Cretaceous several groups of actinopterygians had acquired much more substantial centra in the form of perichordal cylinders of membrane bone. Such groups include caturids (*Neorhombolepis, Macrepistius*), macrosemiids (*Macrosemius, Ophiopsis*), aspidorhynchids (*Belonostomus*) and oligopleurids (*Ionoscopus, Callopterus*). Perichordal, membrane bone centra are also developed in *Polypterus, Lepisosteus, Amia* and Recent teleosts (Gardiner 1983). From this we may conclude that membrane bone centra have developed at least five times within the actinopterygians (*Polypterus, Lepisosteus, Amia*, aspidorhynchids and teleosts) and possibly as many as seven (oligopleurids and macrosemiids).

Simple, ring-shaped centra resembling those of *Amia* are found in several rhipidistians including *Rhizodopsis, Megalichthys, Ectosteorhachis* and *Strepsodus*. But the earliest ossified centra belong to the Devonian dipnoans *Griphognathus, Rhynchodipterus, Soederberghia* and *Chirodipterus*, where they are spool-shaped and presumed to be made up of cartilage bone, as in amniotes.

3. *Ribs*

In some actinopterygians there is a single series of ribs in the wall of the coelom. These are the ventral or pleural ribs and they develop centrifugally from cartilaginous anlagen close to the vertebra. In cladistians and teleosts there are in addition dorsal ribs in the horizontal septum. These develop from cartilaginous anlagen beneath the lateral line, at the outer junction of the horizontal and transverse septa. Many teleosts have yet a further series of ribs, the so-called epineurals in the epaxial musclature.

The dorsal ribs in *Polypterus* are confined to the middle part of the trunk where they are borne on hypertrophied parapophyses. They are peculiar in that they are firmly tied distally to the lateral line scales (Pearson 1981). The dorsal (epipleural) ribs of teleosts, on the other hand, are usually attached by ligaments to the centrum or in the posterior region to the ventral ribs themselves. They are believed to have arisen within the teleosts and to characterize elopocephalans and certain osteoglossomorphs (Rosen *et al.* 1981). Dorsal ribs are a primitive attribute of neither actinopterygians nor osteichthyans. Thus it follows that the ribs of

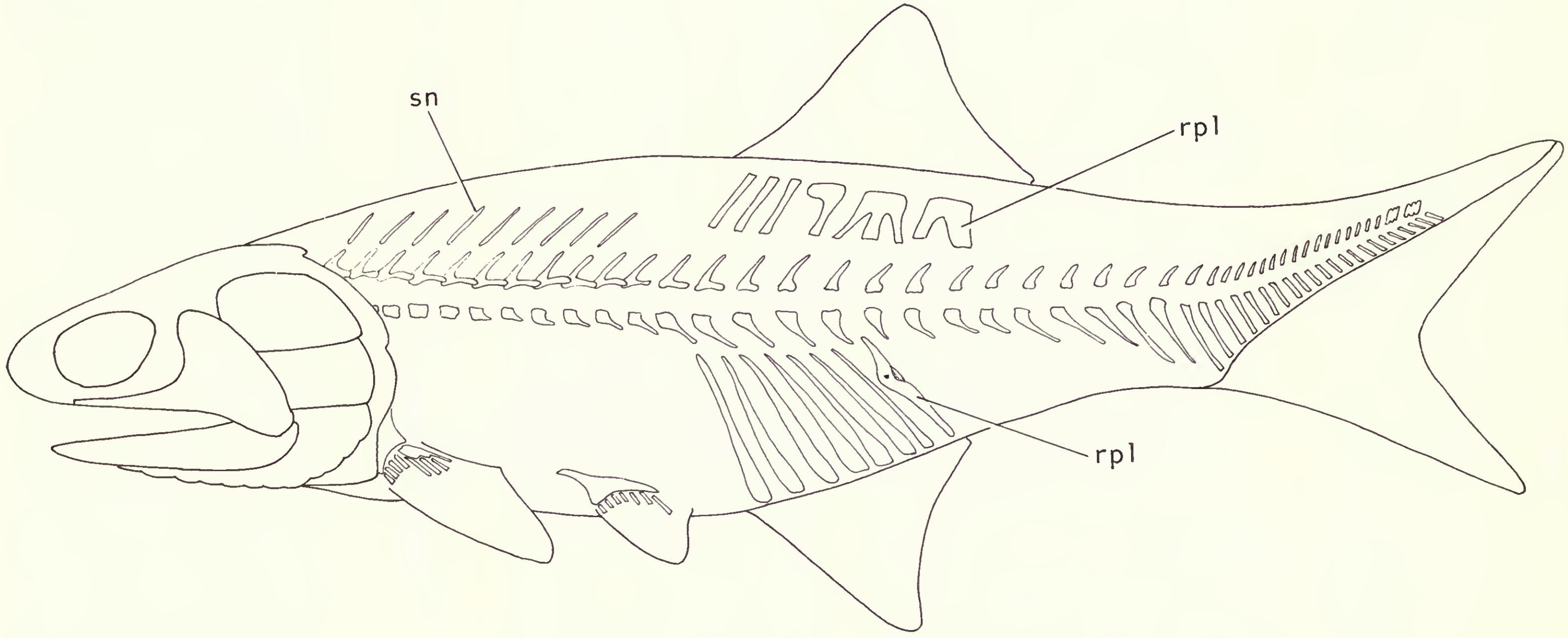

Fig. 124 *Mimia toombsi* Gardiner & Bartram. Attempted restoration of the axial skeleton and endoskeleton of the fins.

chondrichthyans and osteichthyans (other than cladistians and teleosts) are homologous and of the pleural (ventral) type.

Although separate epineural intermuscular (epineural) ribs are synapomorphous for teleosts the primitive condition seems to be an outgrowth or process of the neural arch (Patterson 1973: 237; Rosen *et al.* 1981: 244). They are in the diapophysial position; that is, they are where the bicipital rib of a tetrapod articulates with the base of the neural arch. As Rosen *et al.* (1981) have pointed out, these diapophysial outgrowths in actinopterygians and dipnoans show a morphogenetic gradient which decreases with distance from the occiput; the ribs of primitive tetrapods show a similar gradient.

4. *Supraneurals and neural spines*

Supraneurals are median, cartilaginous or bony structures that lie above the neural spine and the dorsal ligament. They are often confused with median neural spines which may also project above the dorsal ligament but which are formed by the fusion of the right and left halves of the neural arch. The supraneurals may rest on the dorsal ligament (*Lepisosteus*) or articulate with the neural spines (*Acipenser, Protopterus*), or sit on or between the tips of the neural spines (*Leptolepis*, chondrichthyans such as *Notorhynchus*). Primitively they form an extensive series and in *Pteronisculus, Phanerosteon, Hypsocormus* and *Leptolepis* they extend from occiput to dorsal fin. In the porolepid *Glyptolepis* (Andrews & Westoll 1970) they are even more extensive. In many actinopterygians they are confined to the anterior few segments (*Amia, Salmo*) and in others they are missing altogether (*Polypterus*, many teleosts).

Supraneurals are also found in many Recent chondrichthyans, where they are usually confined to the anterior few segments and to the caudal region (= epurals). Occasionally they extend back as far as the anterior dorsal fin and beyond (*Rhina*). Supraneurals are absent in acanthodians.

The neural spines are paired in primitive actinopterygians and median neural spines are considered to be a halecostome characteristic (Patterson 1973: 296). Median neural spines, however, also occur in the caudal region of *Moythomasia, Australosomus, Birgeria* (Nielsen 1949) and *Haplolepis* (Baum & Lund 1974: fig. 1a), as well as of *Polypterus* where they are formed from membrane bone (Gardiner 1983).

Paired neural spines are found in *Acanthodes*, ptyctodonts (personal observation) and many chondrichthyans (*Mustelus, Rhina, Chimaera*), and this is considered to be the primitive gnathostome condition. In other Recent chondrichthyans the neural arches join below the dorsal ligament (*Lamna, Cetorhinus, Squalus*), but in halecostomes, *Eusthenopteron, Griphognathus* and tetrapods they join above it. Median neural spines are also found in the placoderm *Jagorina* (Stensiö 1959: figs 61, 63), the rhipidistians *Thursius, Megalichthys* and *Osteolepis* (caudal region only, Andrews & Westoll 1970: figs 6, 7c, d), *Latimeria*, dipnoans and tetrapods.

Shoulder girdle and pectoral fin

Mimia toombsi

The girdle consists of four paired dermal bones arranged in an overlapping series, post-temporal, supracleithrum, cleithrum and clavicle, with a median interclavicle ventrally. The endoskeletal shoulder girdle is attached to the ventromedial surface of the cleithrum.

The post-temporal (Fig. 125) is a four-sided rectilinear bone which overlaps the supracleithrum posteroventrally. The bone is slightly curved and its anterolateral margin has an unornamented ledge where it is overlapped by the extrascapular. The main lateral line passes through the centre of radiation which lies near the anteroventral corner of the post-temporal.

The supracleithrum is a long, narrow bone which tapers ventrally where it fits over the dorsal tip of the cleithrum. Its centre of radiation lies near the anterodorsal corner and like the post-temporal is pierced by the main lateral line which passes through the bone two-thirds of the way down its posterior margin.

The cleithrum is a large, high bone with a strongly concave anterior margin which forms the

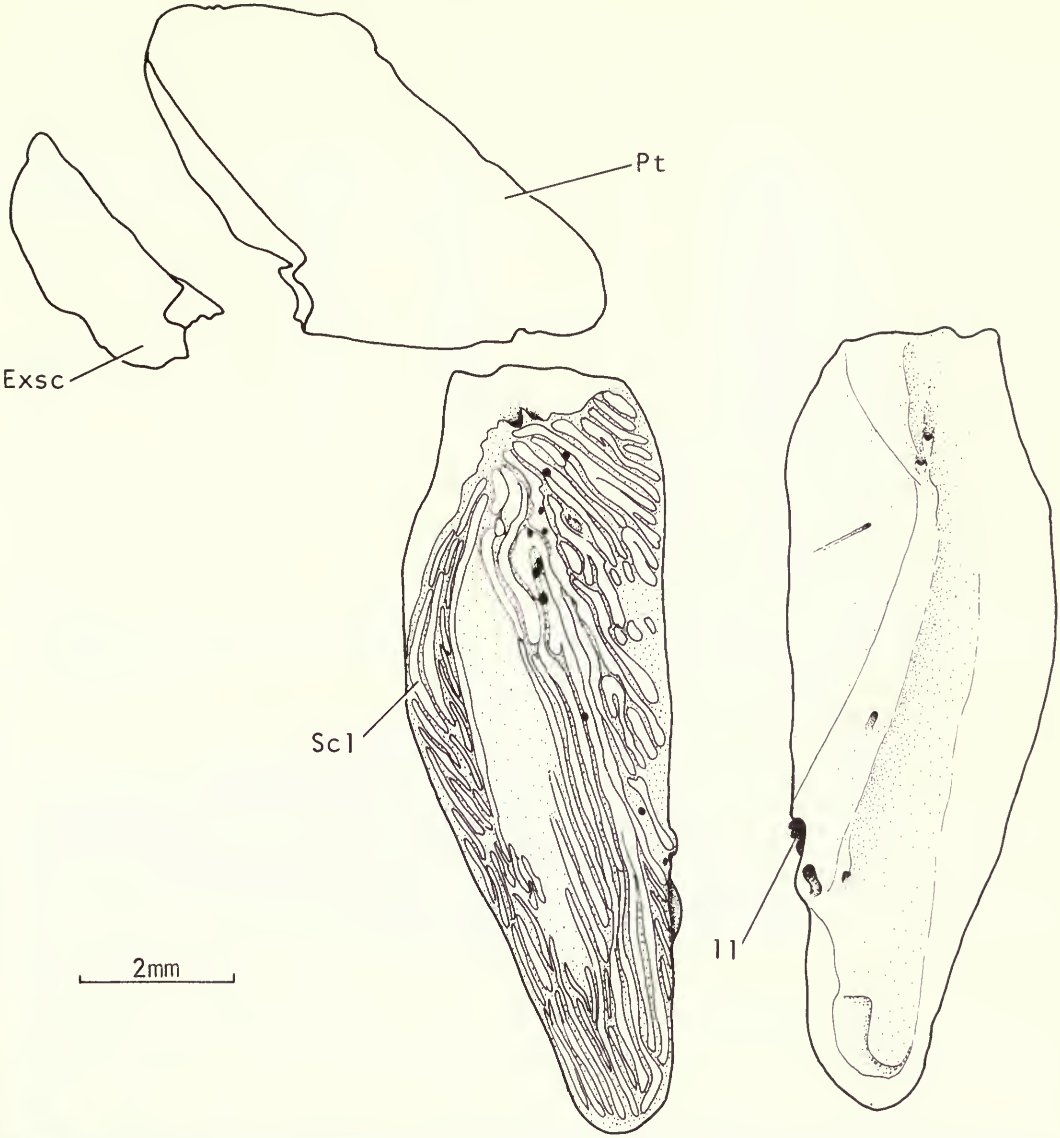

Fig. 125 *Mimia toombsi* Gardiner & Bartram. Left supracleithrum in lateral (left, with outline of post-temporal and extrascapular) and medial views. From BMNH P.56498.

posterior boundary to the branchial cavity. Posteriorly the strongly convex margin is deeply notched ventrally at the point of insertion of the pectoral fin. Ventrally the cleithrum is curved in a medial direction where it is overlapped by the clavicle. The centre of ossification lies anterior and slightly dorsal to the notch for the pectoral fin. The cleithrum is ornamented with stout ridges of ganoine apart from the overlapped areas and the inner edge of the dorsal division.

The clavicle is also a large bone (Figs 126, 130) which curves strongly inwards ventrally, almost to meet its fellow of the opposite side. The clavicle consists essentially of two parts, a large, flat, ventral expanse and a dorsal vertical portion which wraps round the cleithrum. In lateral view the dorsal division is triangular in outline with a long dorsal process. The clavicle is ornamented in the same way as the cleithrum, with long ridges of ganoine. The centre of radiation lies at the junction between the dorsal and ventral divisions. There is no evidence of

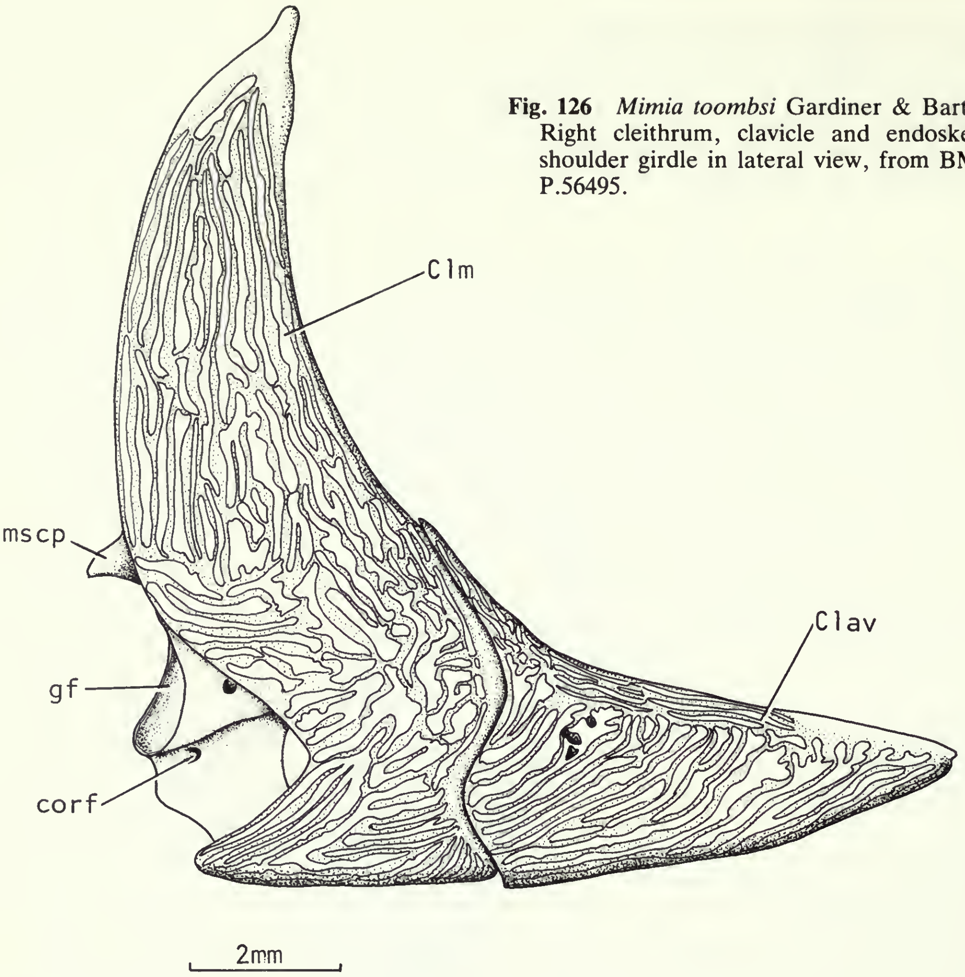

Fig. 126 *Mimia toombsi* Gardiner & Bartram. Right cleithrum, clavicle and endoskeletal shoulder girdle in lateral view, from BMNH P.56495.

the medial process seen in *Acipenser* (Jessen 1972: pl. 15) and said to be present in *Acrorhabdus* (Stensiö 1921: 229).

The interclavicle lies between the clavicles. It is a small ovoid ossification with a few blobs of ganoine along its mid-line.

In cladistians and chondrosteans the two clavicles meet in the mid-line and exclude the interclavicle from the ventral surface (*Acipenser, Scaphirhynchus* Jollie 1980, *Polypterus* Fuchs 1929). This is considered a derived character because an interclavicle similar to that of *Mimia* separates the cleithra in osteolepiforms, porolepiforms, primitive actinistians and tetrapods.

Behind the girdle there is a small postcleithrum (Fig. 127). This bone is little more than a magnified flank scale with a much enlarged peg and a ventral projection. The peg is overlapped by the supracleithrum (Rosen *et al.* 1981: fig. 39B). In *Pteronisculus* the connection with the cleithrum is less intimate and the postcleithrum may only be distinguished from the surrounding flank scales by its slightly larger size. In *Acipenser* (Jollie 1980) the postcleithrum lies largely behind the margin of the supracleithrum and in *Lepisosteus* it is the most dorsal member of a row of modified scales.

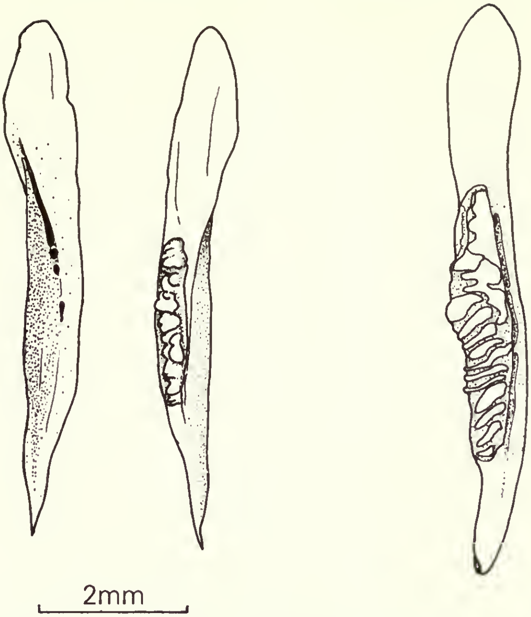

Fig. 127 *Mimia toombsi* Gardiner & Bartram. Postcleithra. (A), right postcleithrum in medial (left) and lateral views, from BMNH P.56484. (B), right postcleithrum in lateral view, from BMNH P.56491.

The endoskeletal shoulder girdle is a single ossification, despite its complex shape. The mesocoracoid arch is well developed and dorsally is directed towards the posterior margin of the cleithrum. In other actinopterygians (except *Moythomasia* and *Acipenser*) the mesocoracoid arch is directed towards the anterior cleithral margin. The dorsal junction of the mesocoracoid arch with the scapular portion is drawn out posteriorly beyond the hind margin of the cleithrum (mscp, Fig. 126), as in *Moythomasia* (Fig. 131). This is the mesocoracoid process and it is also found in *Pteronisculus* (Jessen 1972: fig. 9).

The horizontal middle region of the girdle is produced anteriorly (apr, Fig. 129), as in many actinopterans, and is perforated by two main foramina. The larger, hinder of these is the scapular foramen, that nearer the leading edge of the middle region the anterior scapular foramen. Both foramina occur in *Birgeria, Palaeoniscus, Acipenser, Amia, Elops* and *Salmo* (Jessen 1972). In addition a large coracoid foramen occurs at the junction of the mesocoracoid arch and the coracoid portion of the girdle; this is restricted to fossil actinopterygians.

The radial endoskeleton of the pectoral fin consists of a propterygium, three radials and a metapterygium. These articulate with an almost horizontally-orientated, elongate, glenoid fossa (gf, Fig. 128). The anterior or leading edge of the fin is slightly higher than the trailing edge and the fin is expanded in a horizontal plane much as in *Acipenser, Lepisosteus, Elops* and *Salmo*.

The propterygium is a short, ovoid ossification perforated by a canal. It is embraced by the bases of the marginal rays. The three radials (r, Fig. 137) are a little longer than the propterygium; they are hourglass-shaped, perichondral ossifications. The metapterygium is over twice as long as the radials and supports three short preaxial radials. No distal radials have been observed, but these may have been cartilaginous, as in *Polypterus*, or covered by the proximal ends of the lepidotrichia, as in *Pteronisculus* (Nielsen 1942: 235).

There appear to be 18–20 pectoral rays, the principal of which are only articulated distally. Along the leading edge the terminations of the lepidotrichia alternate with fringing fulcra, as in *Canobius, Mesopoma* and *Rhadinichthys*.

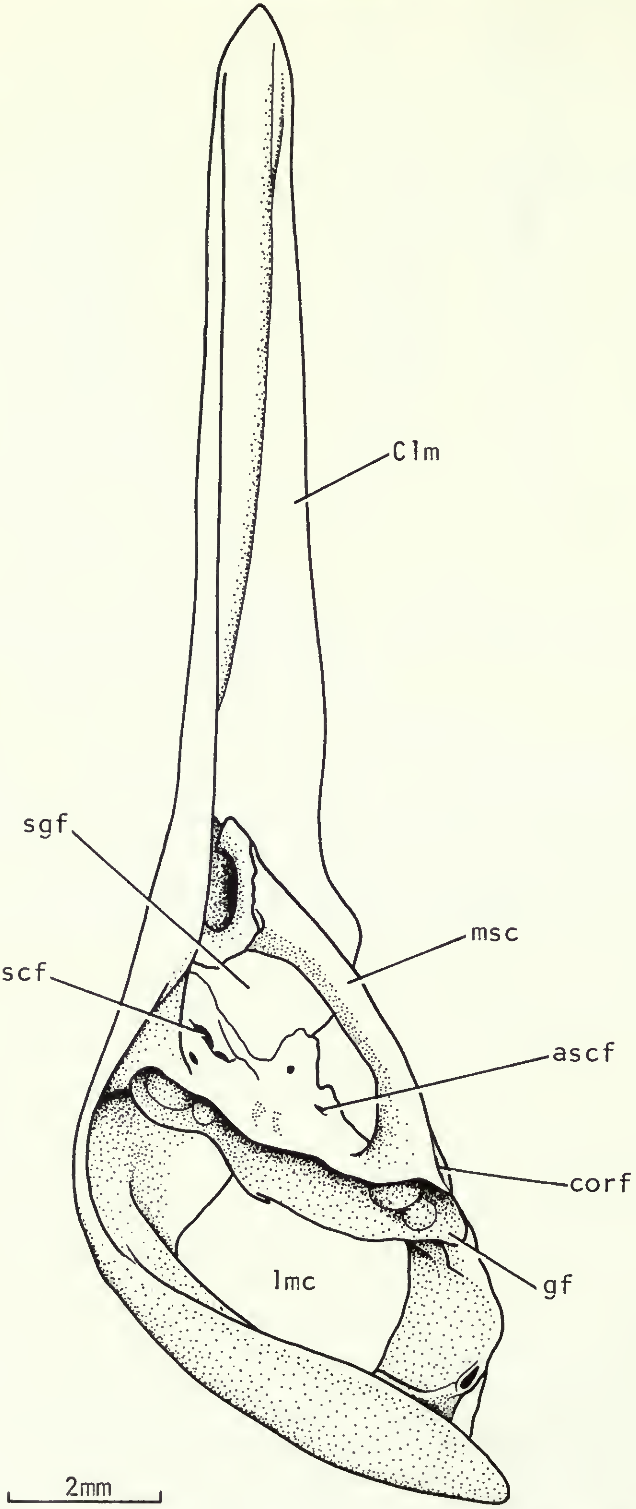
Clm
sgf
msc
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Fig. 128 *Mimia toombsi* Gardiner & Bartram. Left cleithrum and endoskeletal shoulder girdle in posterior view, from BMNH P.53245.

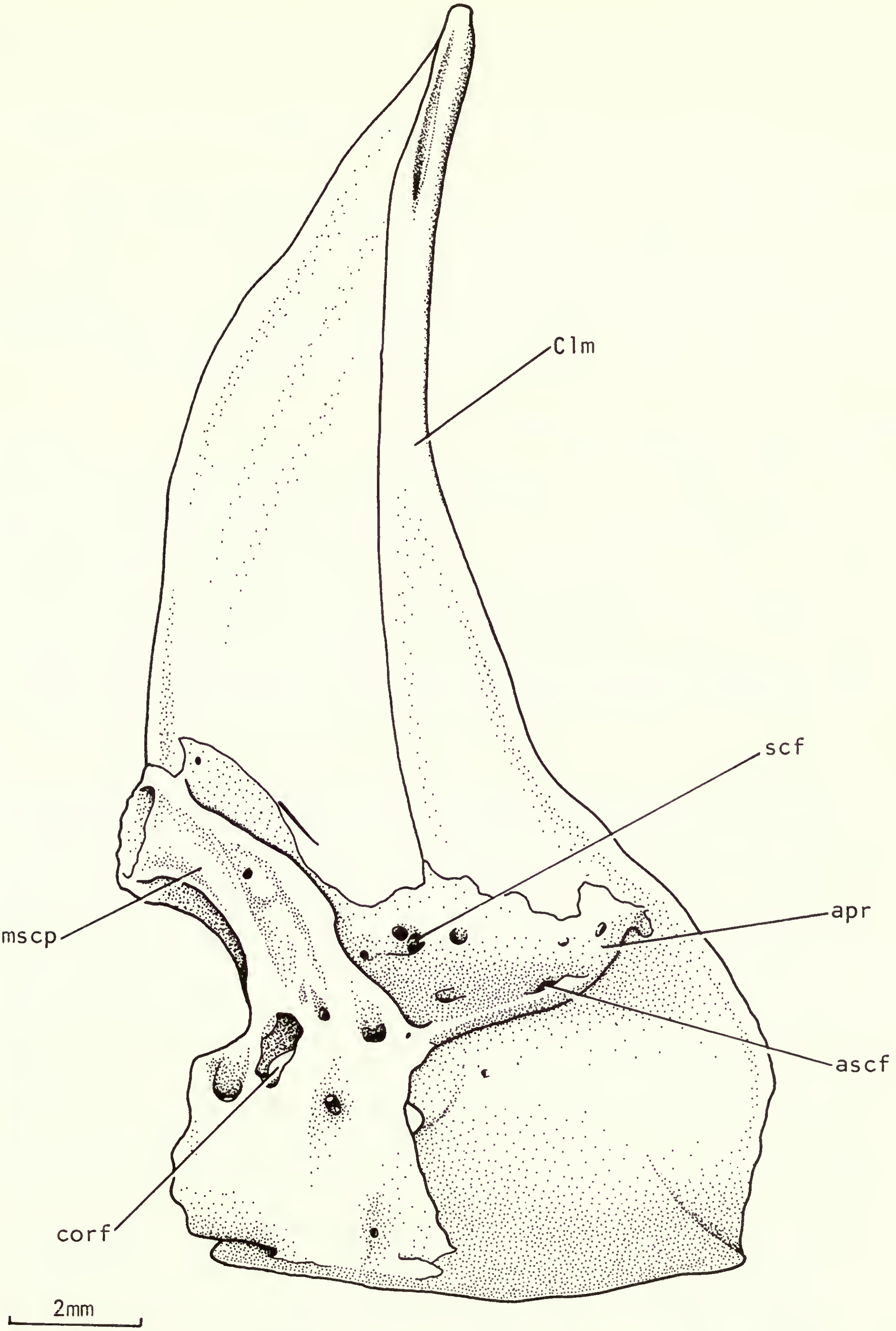
Clm
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Fig. 129 *Mimia toombsi* Gardiner & Bartram. Left cleithrum and endoskeletal shoulder girdle in medial view, from BMNH P.53245.

Moythomasia durgaringa

The pectoral girdle is very similar to that of *Mimia*. The few differences include the size and shape of the postcleithrum and interclavicle, and minor differences in the endoskeletal girdle and fin construction.

The postcleithrum has a much longer, pointed, dorsal peg with an anteriorly-directed process (Fig. 133). The interclavicle is proportionally larger than in *Mimia* and ventrally has two distinct ornamented areas (Figs 134, 135).

In several specimens there is a prominent rostrocaudally-running ridge on the ventral surface of the coracoid region, which marks the subdivision of the ventral fin musculature. A similar ridge is found in *Acipenser, Acrorhabdus, Pteronisculus* (Aldinger 1937, Nielsen 1942), *Perleidus, Pachycormus* and *Elops* (Jessen 1972).

The pectoral fin has a propterygium to which the first three lepidotrichia are attached (Fig. 136) and the first ray is ornamented with longitudinal ridges of ganoine. The remainder of the fin is supported by four radials and a metapterygium. There are 19–24 lepidotrichia, and fringing fulcra occur along the anterior margin, as in *M. nitida* (personal observation).

Shoulder girdle and pectoral fin: discussion

1. *Dermal bones of shoulder girdle*

Primitive actinopterygians show a series of four paired bones plus a median interclavicle, whereas sarcopterygians have five paired bones and an interclavicle. The actinopterygian shoulder girdle differs from that of other osteichthyans in having the cleithrum overlapped dorsally by the supracleithrum. Rosen *et al.* (1981) have argued that this is the primitive osteichthyan condition. In osteolepiforms, actinistians, porolepiforms and dipnoans an extra element, the anocleithrum, separates the supracleithrum from the cleithrum; Jarvik (1944*b*) has hypothesized this to be the primitive osteichthyan condition. Jarvik further suggested that the actinopterygian condition had been arrived at by regression of the anocleithrum. Rosen *et al.* (1981), in contrast, suggested that the anocleithrum developed from the scale-like actinopterygian postcleithrum, and proposed that the incorporation of the postcleithrum (= anocleithrum) as a functional unit in the girdle is a synapomorphy for *Eusthenopteron* and other sarcopterygians.

There is little doubt that the actinopterygian postcleithrum has been derived from the scale row immediately behind the girdle. In *Mimia*, for example, its articulation with the supracleithrum is by an expanded peg, homologous with that on other scales. Further, the postcleithrum in *Polypterus* (Jarvik 1944*b*), *Pygopterus* and *Boreosomus* is little more than the most dorsal member of a modified scale row. A pair of scale-like postcleithra occurs in *Scomber*, but primitive teleosts have three. A postcleithrum is absent in some teleosts and palaeoniscids (*Stegotrachelus, Cornuboniscus, Watsonichthys*), including *Cheirolepis*, where the scales are very small and without peg-and-socket articulations. The absence in *Cheirolepis* is thought to be primitive, as are the small scales devoid of peg-and-socket articulations. Pearson & Westoll (1979) described a postcleithrum in *Cheirolepis*, but re-examination of their material (including BMNH P.41310, P.36061) has failed to convince me of its presence.

A large scale-like extracleithrum is found in fossil actinistians (cf. *Rhabdoderma*, Forey 1981: fig. 7) and is regarded as synapomorphous for that group.

Elsewhere a dermal shoulder girdle is found in acanthodians and placoderms and many attempts have been made to homologize their various dermal elements with those of living forms (Jaekel 1899, 1906; Dean 1907; Jarvik 1944*b*; Stensiö 1944, 1947, 1959). Despite these attempts a separate nomenclature is usually employed for the dermal bones of acanthodians (Miles 1973*b*, Denison 1979) and another for placoderms (Denison 1978).

In acanthodians the shoulder girdle is strengthened by dermal plates and spines both ventrally and laterally. These are best developed in the Climatiidae and Diplacanthidae but are also present in the Gyracanthidae. Dermal plates are wanting in the Ischnacanthidae and Acanthodidae (Miles 1973*b*). The dermal plates, where present, are in two series. Ventrally there is a median unpaired plate (median lorical plate) in *Brachyacanthus, Parexus, Vernicomacanthus* and *Lupopsyrus*, and two median unpaired plates in *Climatius* (Miles

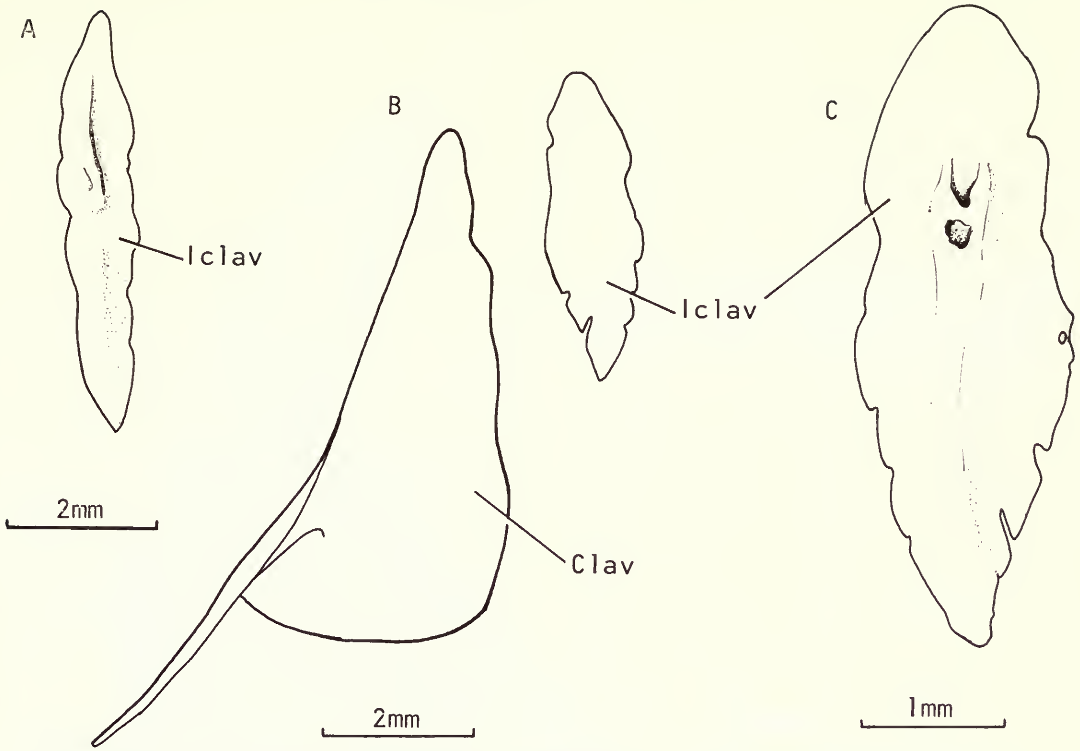

Fig. 130 *Mimia toombsi* Gardiner & Bartram. Interclavicle in (A), (C) dorsal and (B) ventral views. (B) Left clavicle in dorsal view. (A) from BMNH P.56473; (B), (C) from BMNH P.56484.

1973*b*). Ventrolaterally, on either side of the median plate, is a pair of so-called pinnal plates in *Erriwacanthus, Vernicomacanthus, Parexus, Lupopsyrus, Sabrinacanthus, Ptomacanthus, Euthacanthus* and *Gyracanthus*. There are two such pairs in *Brachyacanthus* and *Gyracanthides* and three in *Climatius* (Miles 1973*b*). The pinnals of *Erriwacanthus, Vernicomacanthus* and *Sabrinacanthus* all have extensive ascending laminae.

Dean (1907) suggested that these plates in acanthodians are homologous with the osteichthyan interclavicle and clavicle, whereas Jaekel (1899) homologized them with the cleithrum. Miles (1973*b*: 205) maintained that, although it was possible to compare the ventral bones in climatiiforms with those of the osteichthyan girdle, he found such comparisons imprecise; he concluded that the ventral shoulder-girdle plates of acanthodians and osteichthyans had been independently acquired and that the similarities between them were fortuitous. He also concluded (1973*b*: 162) that there was little possibility of the dermal plates of acanthodians and placoderms being homologous, and so found it necessary to introduce a new terminology for the plates in acanthodians. He came to these conclusions because he assumed that the generalized climatioid pattern comprised two lorical plates and three or four paired pinnal plates, as in *Climatius*. If, however, a single median plate and one pair of lateral plates, as in *Vernicomacanthus*, is the primitive acanthodian condition then the correspondence with the osteichthyan interclavicle and clavicles is far more exact. Moreover, the posterior pinnal plate in *Brachyacanthus* and *Climatius* may be homologous with the spinal plate in ptyctodonts and other placoderms.

Placoderms resemble osteichthyans in having several lateral dermal plates associated with the shoulder girdle and it is probable that it is the short girdle that is primitive for placoderms (Denison 1975), not the elongated thoracic shield of early arthrodires as argued by Gross (1954). The former point of view is supported by the cladograms of placoderm interrelationships put

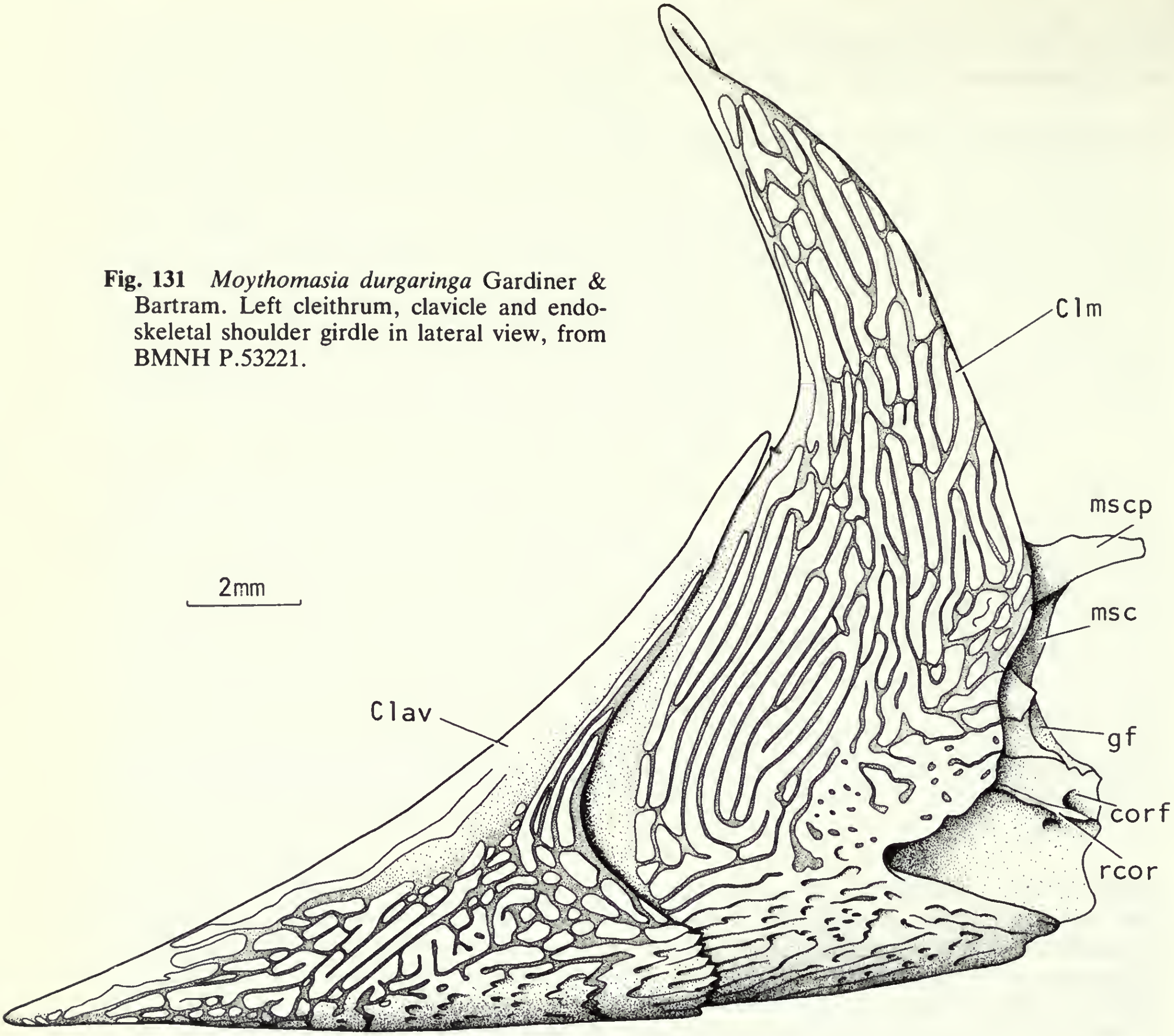

Fig. 131 *Moythomasia durgaringa* Gardiner & Bartram. Left cleithrum, clavicle and endoskeletal shoulder girdle in lateral view, from BMNH P.53221.

forward by Miles & Young (1977) and Young (1980), in which ptyctodonts are considered the sister-group of all other placoderms.

Miles & Young (1977) proposed that the primitive placoderm possessed median dorsal, anterior dorsolateral, anterior lateral, interolateral, spinal, anterior ventrolateral and anterior median ventral plates. Ptyctodonts conform to this pattern apart from the absence of the interolateral.

Jaekel (1906) and Stensiö (1959) homologized the anterior median ventral, anterior ventrolaterals and anterior laterals of arthrodires with the interclavicle, clavicles and cleithra of osteichthyans. Their comparisons would, however, have been more exact had they substituted ptyctodonts for arthrodires. If ptyctodonts are the most primitive placoderms and this sort of outgroup comparison is meaningful, it follows that additional plates must have been added to the thoracic shield within the placoderms (see Young 1980: 69). Furthermore, the anterior edge of the cleithrum (anterior lateral) turns inwards to form a postbranchial lamina in both ptyctodonts and *Romundina* (Ørvig 1975: fig. 2A), much as in osteichthyans.

Stensiö (1959) further homologized the anterior dorsolateral with the osteichthyan post-temporal because of the contact that both were supposed to have made with the

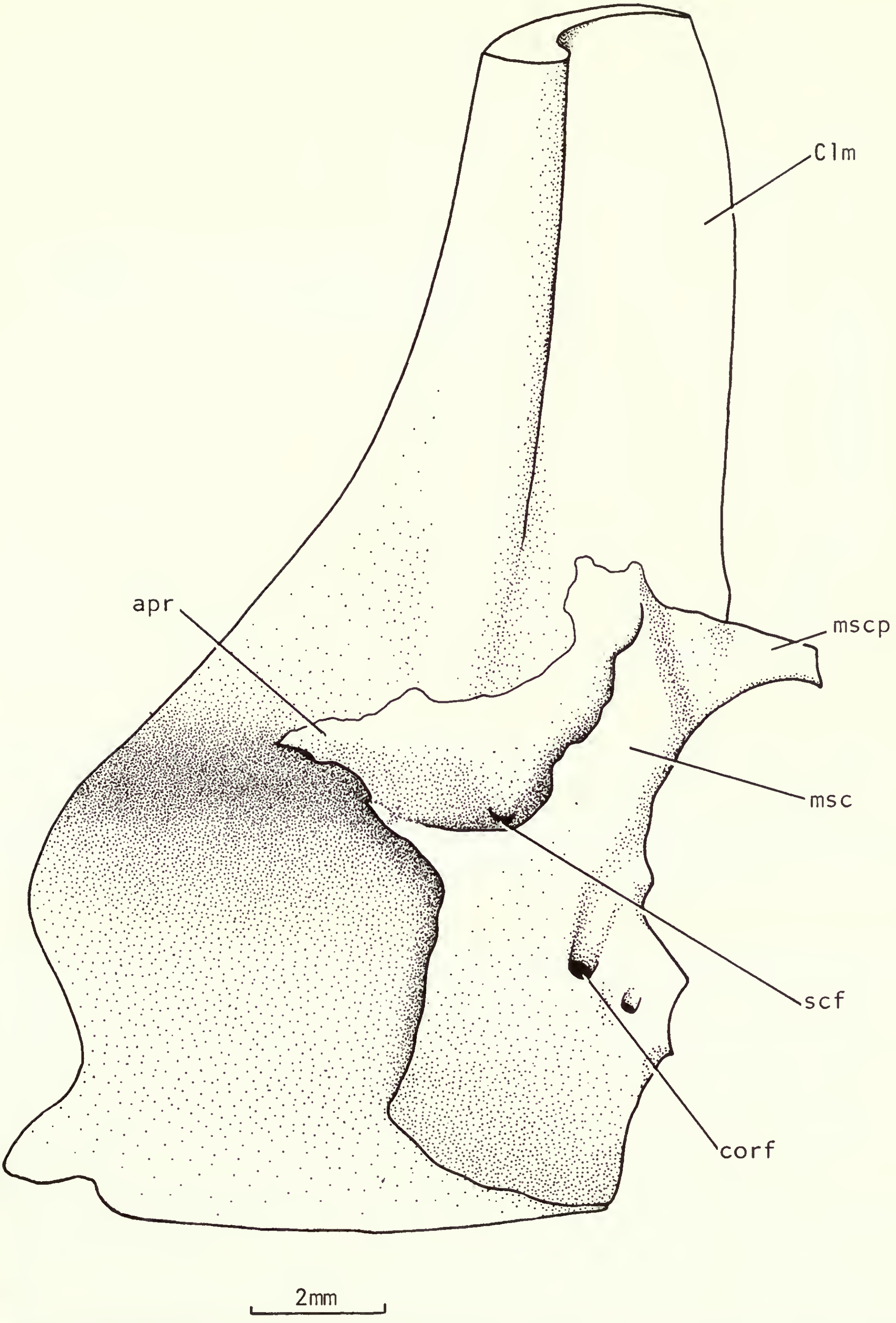
Clm
apr
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Fig. 132 *Moythomasia durgaringa* Gardiner & Bartram. Right cleithrum and endoskeletal shoulder girdle in medial view, from BMNH P.53218.

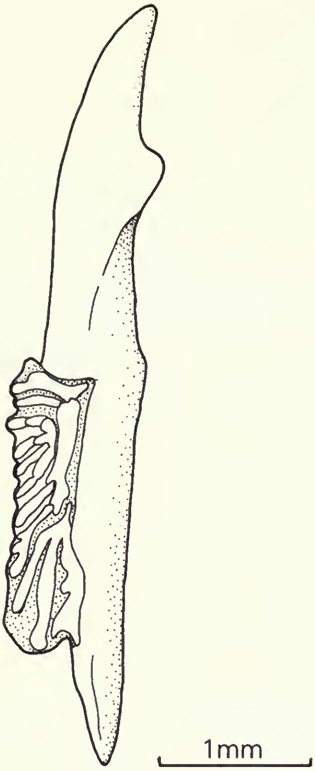

Fig. 133 *Moythomasia durgaringa* Gardiner & Bartram. Right postcleithrum in lateral view, from BMNH P.53256.

neurocranium. But the anterior dorsolateral separates the anterior lateral (cleithrum) and median dorsal and is overlapped by both of these elements.

From this survey I conclude that the presence of ventral dermal plates on the shoulder girdle is synapomorphous for a group including acanthodians, placoderms and osteichthyans, that the cleithrum is a synapomorphy of placoderms and osteichthyans and the anocleithrum a synapomorphy of sarcopterygians.

2. *Endoskeletal girdle*

The actinopterygian shoulder girdle is tripartite and characterized by a middle region with an anterior process (Jessen 1972). The dorsal process is termed the mesocoracoid arch and the dorsomedial muscles of the fin pass beneath it. The anterior diazonal nerves enter the canal formed by this arch and the middle region from in front, and the ventral branches pass through a foramen in its floor. This foramen is called the scapular foramen or posterior canal (Jessen 1972). A separate coracoid foramen for at least one of the ventral branches of a diazonal nerve passes through the medial surface of the scapulocoracoid near the base of the mesocoracoid arch. A separate anterior scapular foramen transmits a branch of the pectoral vein (Jessen 1972). A well-developed anterior process is found in actinopterygians, including *Mimia, Moythomasia, Palaeoniscus, Lepisosteus, Amia, Caturus, Hypsocormus* (Jessen 1972) and teleosts. Pearson & Westoll (1979) have suggested that a middle region is present in *Cheirolepis*, but I am unable to confirm this; however, I have seen remnants of what I interpret as a mesocoracoid arch in BMNH 19428 and P.4345. The shoulder girdle is ossified in one piece (including the mesocoracoid arch) in several actinopterygians, including *Mimia, Pachycormus, Pholidophorus* and *Leptolepis*. In primitive living teleosts, however, it is ossified in three parts, a ventral coracoid, a middle region or scapula and a dorsal mesocoracoid (e.g. *Cyprinus, Mormyrus, Salmo, Elops*). In more advanced teleosts the mesocoracoid arch is lost.

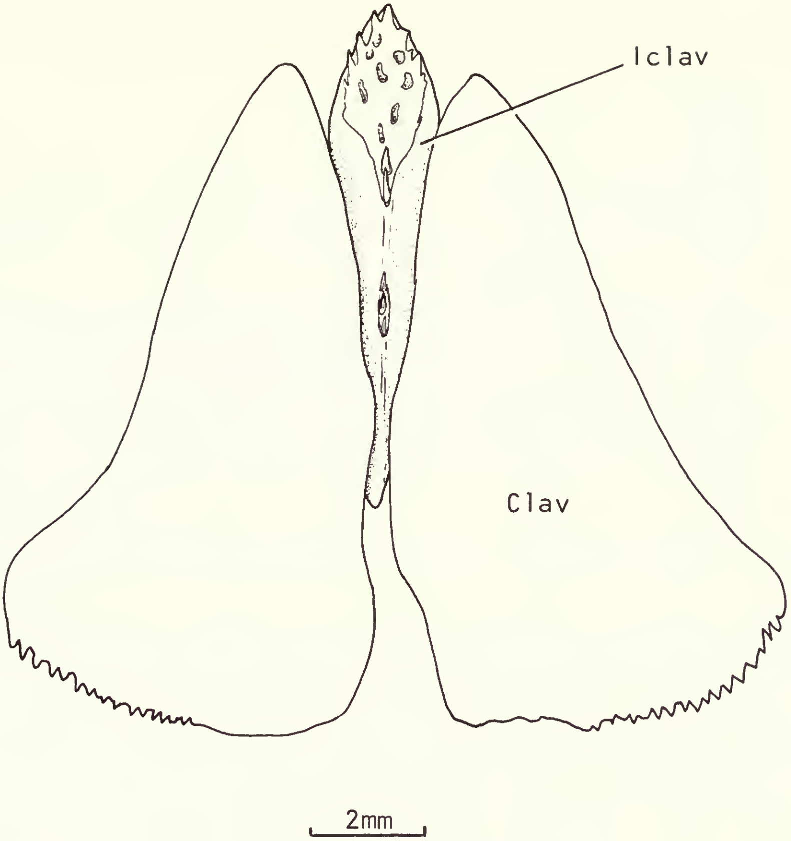

Fig. 134 *Moythomasia durgaringa* Gardiner & Bartram. Clavicles and interclavicle in ventral view, from BMNH P.53219.

Ventrally the tripartite girdle is attached to the clavicle by the anterior coracoid process which forms a canal for the marginal and ventral fin muscles, the supracoracoid foramen. This process and canal are missing in *Amia* and several teleosts (e.g. *Anguilla*).

Both the coracoid process and mesocoracoid arch are missing in *Polypterus* and in common with some teleosts there are two ossifications, the scapula and coracoid. The canal through the girdle of *Polypterus* is thought to be homologous with the coracoid foramen (= posterior canal of Jessen 1972) of other actinopterygians, since it transmits ventral branches of the fourth spinal nerve and posterior arteries and veins of the fin. This canal or foramen passes between the coracoid and scapula in *Polypterus* but through the scapula in teleosts.

A tripartite girdle similar to that of actinopterygians is also found in osteolepiforms (Janvier 1980) and fossil dipnoans (Rosen *et al.* 1981), where the supraglenoid foramen is homologous with the upper muscle canal of Jessen, the supracoracoid foramen with the lower muscle canal and the dorsal buttress with the mesocoracoid arch. The characteristic actinopterygian middle region is represented by the small posterior buttress (Patterson 1982), but unlike actinopterygians there are no apparent nerve foramina. Actinistians on the other hand resemble Recent dipnoans in having an unfenestrated scapulocoracoid which in *Rhabdoderma* (Forey 1981) is represented by a triangular bone resting against the inner surface of the cleithrum.

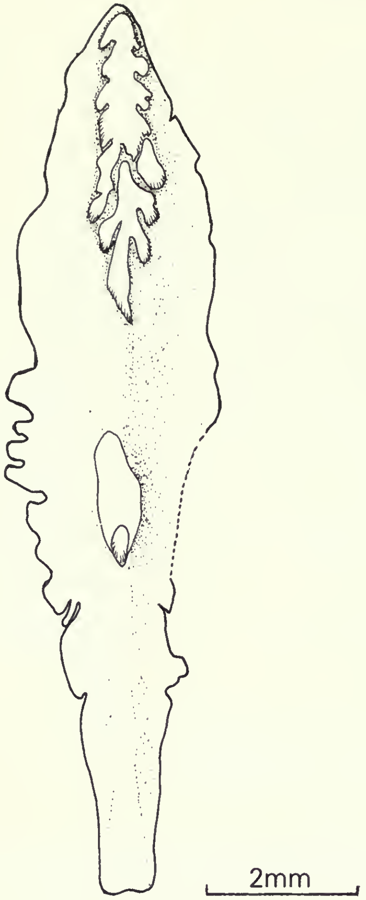

Fig. 135 *Moythomasia durgaringa* Gardiner & Bartram. Interclavicle in ventral view, from BMNH P.56502.

In primitive tetrapods the scapulocoracoid is also ossified in a single piece (e.g. *Eogyrinus, Eryops, Cacops*) and the supraglenoid buttress is homologous with the osteolepiform and dipnoan dorsal buttress and the actinopterygian mesocoracoid arch (Goodrich 1930: 174). In frogs and many amniotes there are two ossifications, referred to as the scapula and coracoid. In yet other amniotes (*Pareiasaurus, Procolophon*, dicynodonts, cynodonts, monotremes) there are three ossifications, with the additional element being referred to as the procoracoid. Thus extant tetrapods and many fossil amniotes resemble *Polypterus* and living teleosts in the retention of sutures between the cartilage-bones in the adult pectoral girdle.

Large size and anterior extent of the middle region of the shoulder girdle characterize actinopterans and the scapular foramen and anterior scapular foramen are synapomorphous for actinopterans. The tripartite girdle with its supraglenoid foramina is synapomorphous for osteichthyans. We may also infer that the primitive number of ossifications in the osteichthyan endoskeletal girdle is three.

In chondrichthyans and acanthodians (*Ptomacanthus* Miles 1973*b*) the two halves of the girdle are connected by cartilage or fibrous tissue, and this may be the primitive gnathostome condition.

In *Acanthodes* (Miles 1973*b*) the scapulocoracoid is perichondrally ossified in three pieces, a large scapulocoracoid (with a hollowed coracoid plate), a small suprascapula and a procoracoid which articulated with the scapulocoracoid and supported the pectoral fin spine. A well-defined canal passes through the scapulocoracoid and opens externally beneath the glenoid fossa *via* the coracoid foramen. This canal is presumed to have transmitted diazonal nerves and vessels.

There are two such canals in *Diplacanthus*, whereas in *Sabrinacanthus* (Miles 1973*b*) there are numerous fine foramina ramifying through the posteroventral region of the scapulocoracoid, as in some placoderms.

In chondrichthyans (e.g. *Hexanchus, Pristiurus, Chimaera*) there is usually a single, internal coracoid foramen for the diazonal nerves, but this soon divides and opens externally above and below the glenoid fossa. The coracoid foramen is also seen in *Acipenser* and other actinopterans, as well as many tetrapods, and is consequently considered to be a primitive gnathostome feature. The external upper opening is called the supraglenoid foramen, but this is not homologous with the similarly-named canal in osteichthyans (see p. 378). The coracoid region expands immediately below the pericardium and there is a distinct coracoid fossa beneath the glenoid fossa, as in *Acanthodes*, for the ventral fin musculature.

There is considerable variation in the pectoral endoskeleton of placoderms and in the presumed advanced forms the scapulocoracoid is a low structure lacking a prominent scapular blade (arthrodires). Pseudopetalichthyids, rhenanids and arthrodires (Broili 1933, Stensiö 1959, Young 1980) have an extensive anteriorly-directed coracoid process and arthrodires have an elongated glenoid fossa. The long, low scapulorocacoid of arthrodires is crossed by a series of diazonal nerves and segmented vessels. An extensive coracoid process is seen elsewhere in acanthodians (*Sabrinacanthus*), chondrichthyans and actinopterans and is probably primitive, as Miles (1973*b*) suggested.

A scapular process is found in *Pseudopetalichthys*, certain rhenanids (*Brindabellaspis, Jagorina*) and ptyctodonts. This is regarded as a primitive gnathostome feature as suggested by Young (1980: 51).

In ptyctodonts there is a canal for the ventral fin musculature, bounded externally by the clavicle (anterior ventrolateral plate, Miles & Young 1977). This canal is homologous with the supracoracoid foramen of osteichthyans and is inferred to have been formed by a plate of dermal bone bridging the coracoid fossa. In osteichthyans it is bounded by the cleithrum, except in *Acipenser* where the clavicle forms its anterior margin. In *Rhynchodus* (Stensiö 1959: fig. 75) the identical canal has a rim of perichondral bone posteriorly. A similar ventral fossa also occurs in the palaeacanthaspids *Romundina* (Ørvig 1975: pl. 5) and *Palaeacanthaspis* (Stensiö 1944: fig. 9), but here it is closed anteriorly by perichondral bone. This canal or fossa is absent in other placoderms but nevertheless is regarded as a synapomorphy of a group containing placoderms and osteichthyans. In ptyctodonts the endoskeletal girdle and glenoid fossa project posteriorly beyond the dermal girdle, much as in actinopterygians, and the pectoral fin is similarly orientated in both groups.

A coracoid foramen has been recorded in *Brindabellaspis* (Young 1980) and *Romundina* (Ørvig 1975: pl. 4, dzv).

3. *Pectoral fin*

The pectoral fin of actinopterygians is characterized by having a propterygium (Rosen *et al.* 1981), a first radial which is short, broad and strongly articulated. In *Mimia, Moythomasia, Palaeoniscus, Pteronisculus, Acipenser, Lepisosteus* and most actinopterygians (Patterson 1982) the propterygium is perforated by a canal which in living forms conducts nerves and vessels (Jessen 1972). A perforated propterygium is an actinopteran character (Patterson 1982).

A well-developed propterygium is also found in *Cheirolepis* (Ra_2, Ra_3 of Pearson & Westoll 1979: fig. 13) where it is clasped by four lepidotrichia (BMNH P.6096a). There is no evidence of a propterygial canal and in this respect *Cheirolepis* resembles *Polypterus*.

Rosen *et al.* (1981) have interpreted actinopterygian paired fin structure as a transformation of a metapterygial fin into a propterygial type. Certainly, pectoral metapterygial elements are still to be found in such primitive members as *Cheirolepis* (personal observation), *Mimia, Acipenser, Pteronisculus* and *Palaeoniscus* (Jessen 1972), and from a study of the development of *Polypterus* (Budgett 1902) much of the fin in this fish also appears to be metapterygial.

Two sets of radials usually occur in the pectoral fins of actinopterygians. Posteriorly in sturgeons and on the second radial of *Elops* there are three sets. The distal radials are triangular in shape and sit between the tips of the proximal radials in primitive forms.

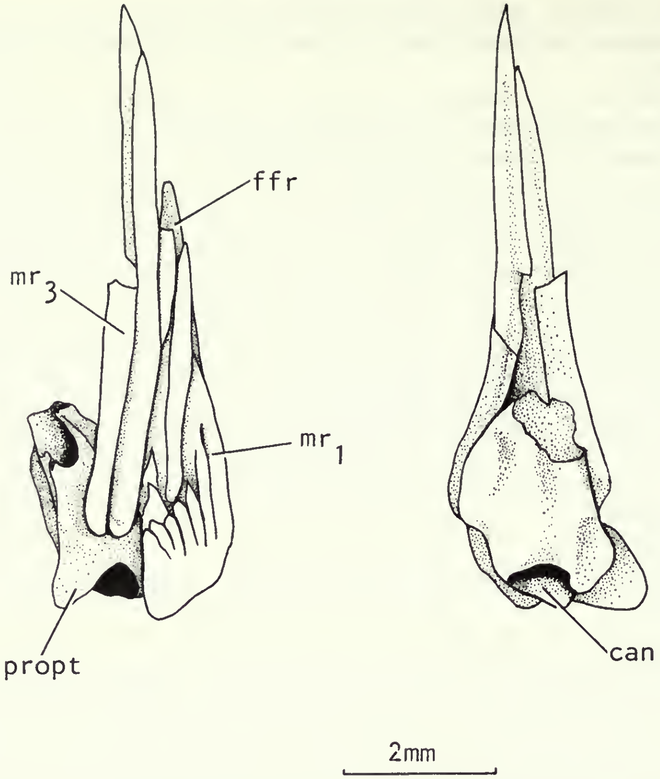

Fig. 136 *Moythomasia durgaringa* Gardiner & Bartram. Propterygium and leading fin-rays in external (left) and internal views, from Western Australian Museum no. 70.4.244 (holotype).

The bases of the marginal rays embrace the propterygium in actinopterygians and in *Moythomasia* and teleosts the first ray, at least, is attached to it. The first condition is considered synapomorphous for actinopterygians.

Pelvic girdle and fin

Mimia toombsi

The fin is small and situated about midway between the pectoral and anal fins. Only one specimen contains traces of the pelvic girdle. The pelvic plate is smaller than in *Moythomasia* and is without an anteromedial process. No radials were observed. The fin consists of around 20 lepidotrichia.

Moythomasia durgaringa

The pelvic plate (Pg, Fig. 138) is a thin, triangular, perichondral ossification with a slender anteromedial process. Seven radials articulate with its posterior margin. The six anterior radials are of approximately the same size, but the seventh, the most posterior, is much larger and is presumed to represent the metapterygial axis. Seven radials have been recorded in *Acipenser* (Rosen *et al.* 1981: fig. 28B), eight in *Boreosomus* (Nielsen 1942), nine in *Scaphirhynchus* and as many as 14 in *Polyodon*. *Polypterus* has only four.

The pelvic fin is nearer to the anal than to the pectoral (cf. *M. nitida* Jessen 1968: fig. 4) and contains 18–20 jointed lepidotrichia. It bears fringing fulcra along its anterior edge.

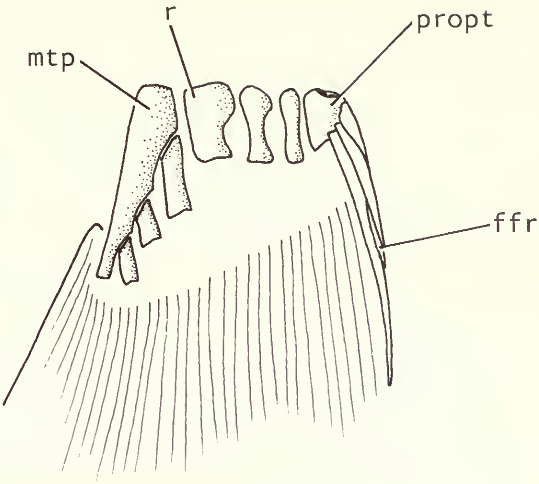

Fig. 137 *Mimia toombsi* Gardiner & Bartram. Reconstruction of the base of the right pectoral fin in dorsal view, from several specimens.

Pelvic girdle and fin: discussion

The pelvic fin in actinopterygians appears to be constructed differently from the pectoral (Goodrich 1930), whereas in all other osteichthyans the two are similar in structure. Davidoff (1880) reasoned that this was because in actinopterygians the metapterygial skeleton of the pelvic fin had shifted inwards and been incorporated in the pelvic girdle. Rosen *et al.* (1981) revived Davidoff's theory as it offered an explanation of the observed similarity between the pelvic endoskeleton of chondrosteans and the metapterygium plus preaxial radials of chondrichthyans and because the alternative, that the chondrosteans possess the most primitive paired fins, violated the monophyly of osteichthyans and actinopterans. They further reasoned that actinopterygians might not have a primary pelvic girdle.

In *Polyodon, Scaphirhynchus, Acipenser* and some palaeoniscids (Lehman 1966) there is a series of rod-like basal cartilages which are presumed to represent the segmental metapterygial skeleton. These fuse in most adults but may remain separate in some palaeoniscids and partially separate in *Scaphirhynchus*. Two rows of cartilages are joined to the outer surface of these internal cartilages, an inner row of elongate radials and a distal row of smaller triangular radials.

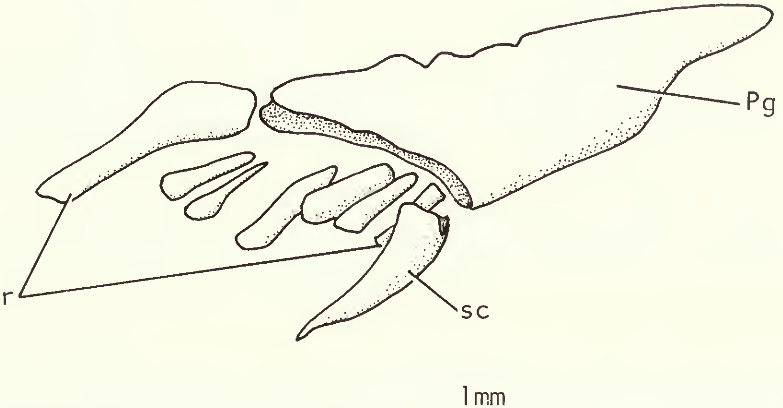

Fig. 138 *Moythomasia durgaringa* Gardiner & Bartram. Pelvic girdle and radials of the right side in dorsolateral view, from BMNH P.53236.

Two rows of radials also occur in *Polypterus, Pteronisculus, Boreosomus, Pygopterus* and many other palaeoniscids, and also in *Lepisosteus* and *Amia*, but in teleosts there is only a single series. There are some 14 proximal radials in *Polyodon*, ten in *Pteronisculus*, nine in *Scaphirhynchus*, eight in *Boreosomus*, seven or eight in *Acipenser* and four in *Polypterus*. In *Lepisosteus, Amia* and primitive teleosts the radials are reduced to never more than three small nubbins, and in many teleosts there is no trace of radials.

I conclude, like Patterson (1982), that a pelvic plate and two series of radials are synapomorphous for actinopterygians.

Median fins

Mimia toombsi

The dorsal fin lies in the posterior half of the body opposite the anal fin (Fig. 145). Remnants of the endoskeleton of the median fins are found in several specimens, but owing to the post-mortem folding and twisting of the body exact relationships of individual ossifications are difficult to determine. Nevertheless, both dorsal and anal fins appear to be supported by a single series of radials.

In the dorsal fin the few anterior radials are rod-like; posteriorly the fin is supported by three compound radial plates (rpl, Fig. 124). These posterior plates correspond in part to the single axonost plates described in *Pygopterus, Pteronisculus, Birgeria* and *Australosomus* (Aldinger 1937, Nielsen 1942, 1949). The dorsal fin has 28–36 branched, segmented lepidotrichia and on the leading edge fringing fulcra alternate with the lepidotrichial endings.

The anal fin is supported by seven long radials which are expanded distally and there is a single complex radial plate posteriorly. This radial plate (rpl, Fig. 124) has lateral wing-like extensions proximally and these are perforated by a small foramen. A much larger foramen passes through the centre of the radial plate. The anal fin is made up of 30–40 branched, segmented lepidotrichia.

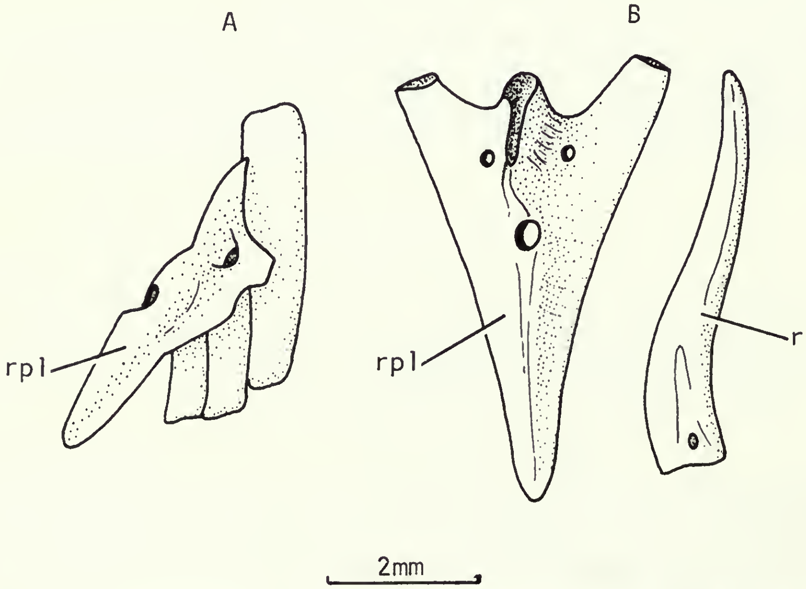

Fig. 139 (A), anal radials and anal radial plate of *Mimia toombsi* Gardiner & Bartram in right lateral view, from Western Australian Museum no. 70.4.245 (holotype). (B) *Moythomasia durgaringa* Gardiner & Bartram, anal radial plate in dorsal view, anal radial (right) in lateral view, from BMNH P.53218.

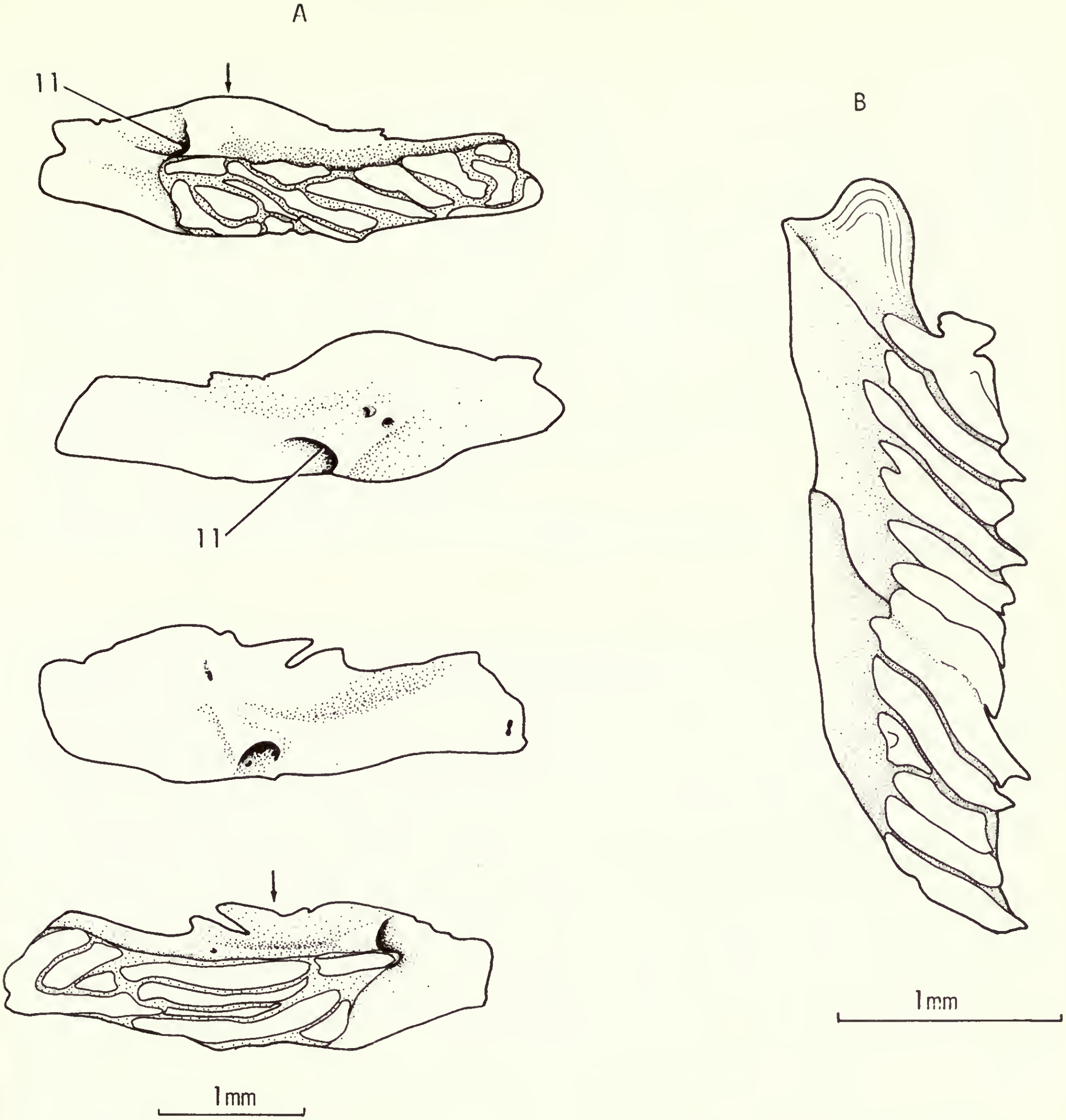

Fig. 140 *Mimia toombsi* Gardiner & Bartram. (A), two lateral line scales in lateral and medial views (arrow marks anterior), from BMNH P.56497. (B), two articulated, anterior trunk scales, from BMNH P.56495.

The caudal fin is deeply cleft and inequilobate and the lepidotrichia are closely set, branched and jointed. There are some 50 or more lepidotrichia and along the ventral margin the lepidotrichial endings alternate with fringing fulcra.

Moythomasia durgaringa

The dorsal and anal fins are opposite to one another, nearer to the tail than the head. The dorsal fin is slightly longer than that of *Mimia* with around 40 lepidotrichia, but the anal fin is of comparable size (30–35). A similar radial plate is present at the rear of the anal fin (rpl, Fig. 139); it only differs from that of *Mimia* in the possession of a posteriorly-directed distal flange.

The caudal fin has around 80 lepidotrichia and the ventral margin supports fringing fulcra.

Median fins: discussion

1. *Dorsal and anal fins*

Most actinopterygians have a single dorsal and anal fin, but many teleosts also have an adipose dorsal fin which may be supported by actinotrichia. Other teleosts may have as many as three dorsal and two anal fins (*Gadus*) and a continuous dorsal fin is seen in many palaeoniscids (e.g. *Tarrasius*) and teleosts (gymnotids, anguillids).

The dorsal and anal fins are supported by a series of parallel radials which are often arranged in three series (each radial is three-segmented). The radials beneath the dorsal and anal fins are three-segmented in chondrosteans, many palaeoniscids (*Birgeria, Pteronisculus, Boreosomus*), *Lepisosteus, Amia* and several teleosts (e.g. osteoglossids, cyprinids, salmonids, esocids), and are two-segmented in *Tarrasius, Australosomus* and many other teleosts (gadids, characinids, clupeids; Bridge 1896). In *Polypterus* the dorsal fin is supported by a single series but in the anal fin all the radials, apart from the first, are in two parts. The lepidotrichia clasp the ends of the radials forming modified ball-and-socket joints in neopterygians, where the distal radials are spherical. Posteriorly some of the distal dorsal and anal radials are compounded into an axonost or radial plate in *Mimia, Pteronisculus, Birgeria, Pygopterus* and *Australosomus* (Nielsen 1942, 1949).

Primitively the fin-rays far exceed the radials in number, but in neopterygians, haplolepids, perleidids, *Bobasatrania, Luganoia* and *Platysiagum* (Patterson 1973) the number of dorsal and anal fin-rays is equal to that of their supports.

2. *Caudal fin*

The caudal fin in actinopterygians is primitively heterocercal, although a small epaxial lobe occurs near the tip of the tail in several adult palaeoniscids (*Cheirolepis, Palaeoniscus, Paramblypterus*) and is present in the ontogeny of Recent forms where it is supported by actinotrichia. In palaeoniscids it is supported by small lepidotrichia. Large epaxial fin-rays are developed in saurichthyids, amiids, pholidopleurids, pycnodonts, pachycormids and other teleosts (excluding pholidophorids). If the published phylogenies are correct (Patterson 1973, 1977*a*) they must have been independently developed on at least six occasions.

In living chondrosteans there is a series of median epurals lying above the neural arches of the tail; these are believed to be serial homologues of the supraneurals (Patterson 1973).

In advanced actinopterygians the tail is homocercal and in halecomorphs and teleosts the epaxial fin-rays are supported by a few epurals. There are seven epurals in pachycormids, six in *Australosomus*, four or five in *Amia* and three or fewer in living teleosts (Patterson 1973). In pycnodonts the epaxial fin rays are apparently supported by the neural arches (Gardiner 1970).

In *Polypterus* there is no sure way of distinguishing between radials and epurals or between dorsal fin-rays and epaxial caudal rays; nevertheless in development there appear to be three epurals.

The hypaxial lobe in actinopterygians is supported mainly by the expanded haemal spines and hypurals. The hypaxial radials are reduced to small nubbins of bone or cartilage at the tips of these spines. Reduced hypaxial radials are found in palaeoniscids (*Pteronisculus*), chondrosteans, *Lepisosteus* and primitive teleosts. Radials are absent in *Polypterus* and the hypaxial lobe is supported solely by expanded haemal spines and hypurals. In actinopterygians the lepidotrichia clasp the spines and hypurals, as well as the radials where present.

Squamation

Mimia toombsi

The body is entirely covered with scales, which have a transverse course up to the inversion line at the base of the tail. There are approximately 75 transverse scale rows between the cleithrum and the line of inversion. Ridge scales completely clothe the dorsal margin and the area between the anal fin and the tail. There are ten ridge scales in front of the dorsal fin, two in front of the anal fin and eight between the anal and the tail. Those on the caudal fin form a rigid cutwater and extend right to the tip of the tail. All the ridge scales are median structures.

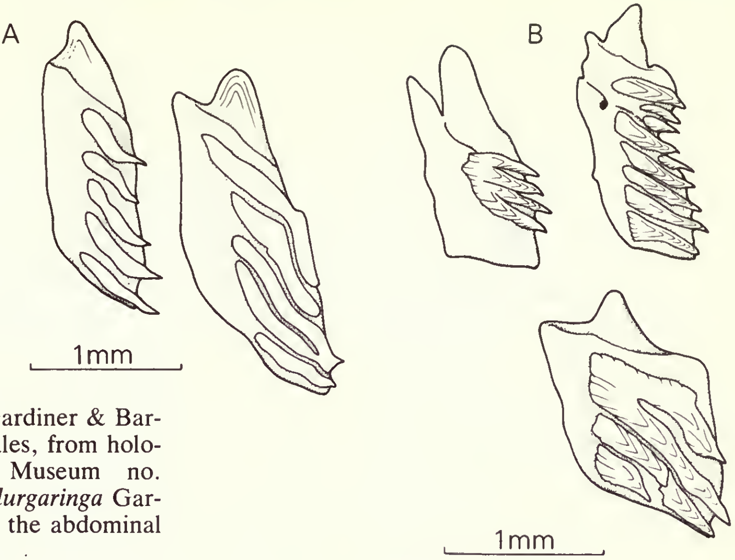

Fig. 141 (A), *Mimia toombsi* Gardiner & Bartram, posterior abdominal scales, from holotype, Western Australian Museum no. 70.4.245. (B), *Moythomasia durgaringa* Gardiner & Bartram, scales from the abdominal region, from BMNH P.56479.

The lobe of the pectoral fin is not scaly (cf. *Polypterus, Cheirolepis*), but the points of insertion of all the fins are marked by bands of much narrower scales.

The scales themselves have a deeply incised hinder margin and are ornamented with short ridges of ganoine which terminate posteriorly in sharp points. On the anterior trunk scales there are 7–10 stout ridges of ganoine, but posteriorly the number is reduced to four or five and near the base of the tail to one. They have well-marked peg-and-socket articulations, with the peg exhibiting growth lines (Pl. 2c). The lateral line scales are higher than broad and the lateral line canal enters the scale anteriorly at the junction of the peg with the anterodorsal ornamentation (Fig. 140A).

The scales have a diagonal long axis (see Gross 1966) and a reduced bony base (Fig. 143). Both dentinal tubules and dentine are apparently wanting and the cell spaces are exceptionally large. The ganoine layer is relatively thick and quite unlike that of any other actinopterygian. The ganoine is in the form of superposed generations which appear to have grown in an aberrant 'onion-skin' fashion without an accompanying layer of dentine. Judged by presumed younger individuals the ganoine first forms longitudinal ridges or blisters, completely separate from one another. These later fuse by the addition of further superficial layers of ganoine. The bony base consists of horizontal layers with contained cell spaces, canals of Williamson and canals for fibres of Sharpey.

Moythomasia durgaringa

There are far fewer transverse scale rows than in *Mimia*, with a scale count of between 44 and 48.

The scales are ornamented by ridges of ganoine which branch and anastomose. The ridges terminate posteriorly in up to 14 serrations on the more anterodorsal flank scales, but anteroventrally the scales have fewer serrations (eight or nine). Posteriorly the scales have five or fewer serrations. Behind the pelvic fin there is a pair of elongate, almost oval cloacal scales, equal in area to approximately three normal scales (BMNH P.53217).

Initially there are separate ridges of dentine and ganoine (Fig. 141B) and new ganoine and dentine are added between the ridges until the whole external exposed surface is ganoine-covered. The ganoine is single-layered over most of the scale, and this is presumed to be primitive (Schultze 1977). Superposed generations of buried ganoine are confined to the scale margins (Fig. 144) and to the edges of the primary ganoine ridges. The scales have a diagonal axis and a reduced bony base. The bony base contains cell spaces and canals for fibres of

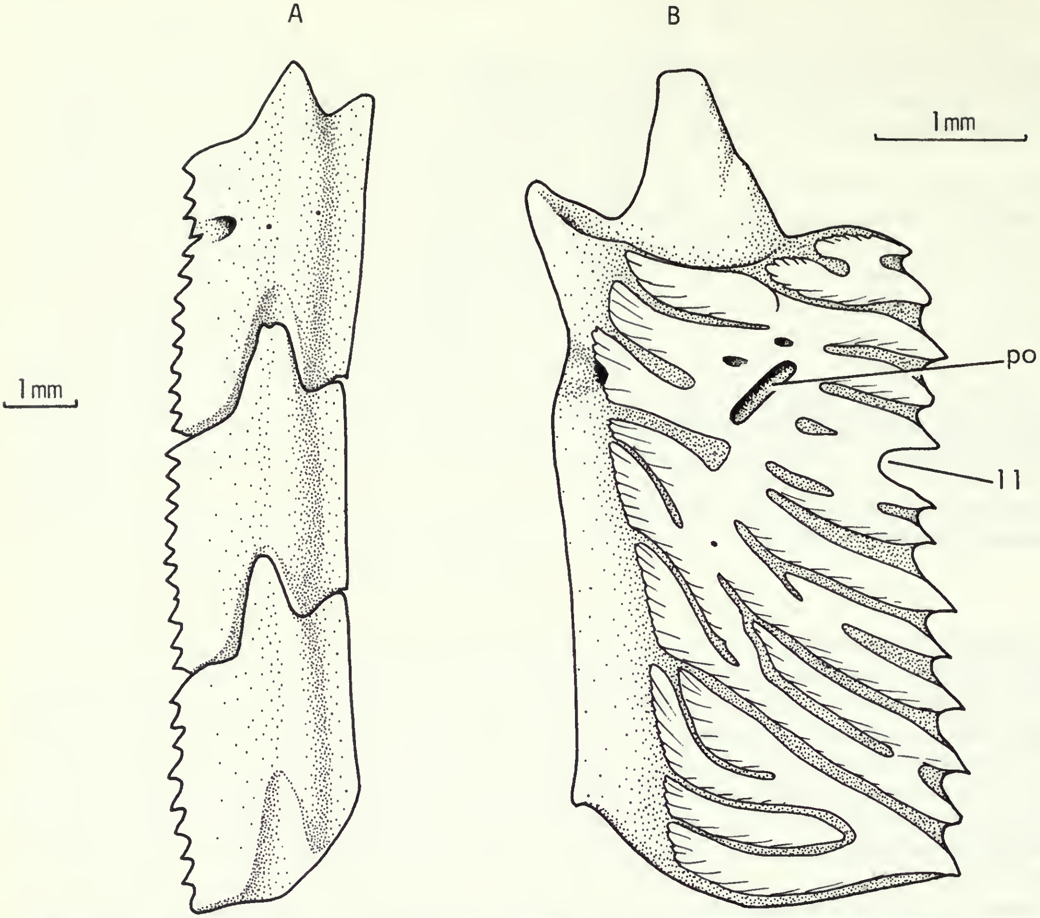

Fig. 142 *Moythomasia durgaringa* Gardiner & Bartram. (A), three scales in articulation, including the lateral line scale, medial view, from BMNH P.53221. (B), lateral line scale in lateral view, from BMNH P.53221.

Sharpey. Above the base is a horizontal vascular canal system from which the dentinal tubules pass upwards through the dentine layer.

The lateral line scales have surface pores and the ventral medial surface of the scales has a distinct depression for the articulatory peg of the scale immediately below it. The ornamentation is very variable and corresponds closely with that of *M. perforata* (Gross 1953: fig. 5).

Squamation: discussion

1. *Scale structure*

The scales of generalized actinopterygians are of the ganoid type in which the whole scale typically has an 'onion-skin' mode of growth, with new material being added concentrically to both the outer and inner surfaces. Bone is added to the base of the scale and ganoine to the surface, and the scale becomes thick and shiny. In advanced actinopterans the ganoine is pseudoprismatic (Ørvig 1967*a*, 1978) and in many teleosts is lost altogether.

In *Cheirolepis* (Gross 1967) the growth lines indicate that the layers of ganoine are added mainly to the anterior margin.

In *Polypterus* the superposed generations of buried ganoine are confined to the circumference (Meinke 1982: 371), but as in *Cheirolepis* they are most prominent on the anterior

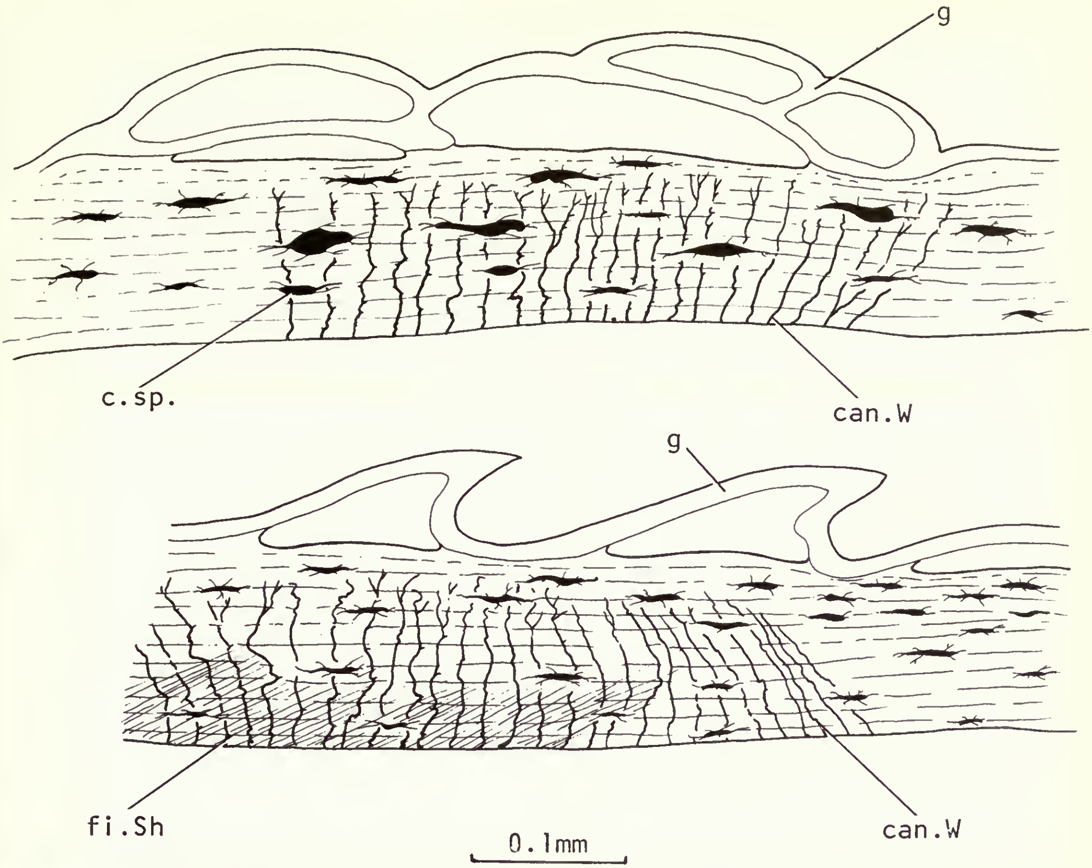
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Fig. 143 *Mimia toombsi* Gardiner & Bartram. Vertical longitudinal sections through two flank scales. From BMNH P.56503.

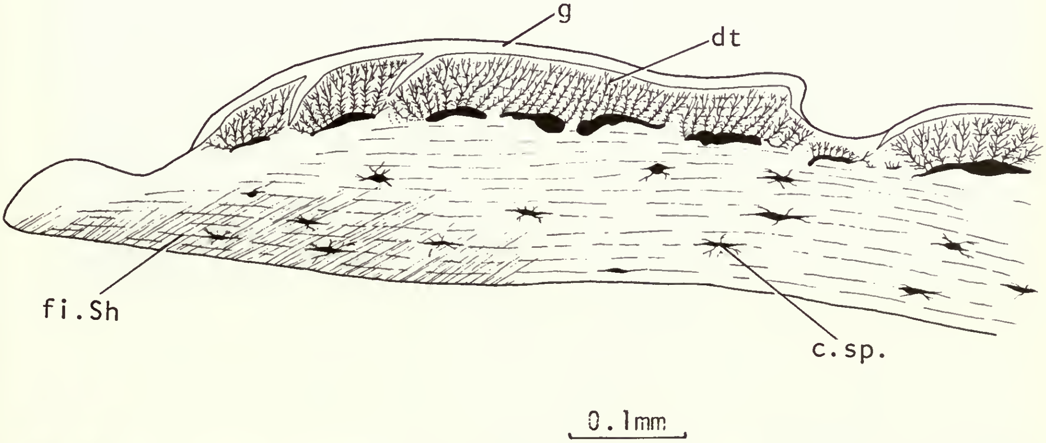
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Fig. 144 *Moythomasia durgaringa* Gardiner & Bartram. Vertical longitudinal section through flank scale. From BMNH P.53221.

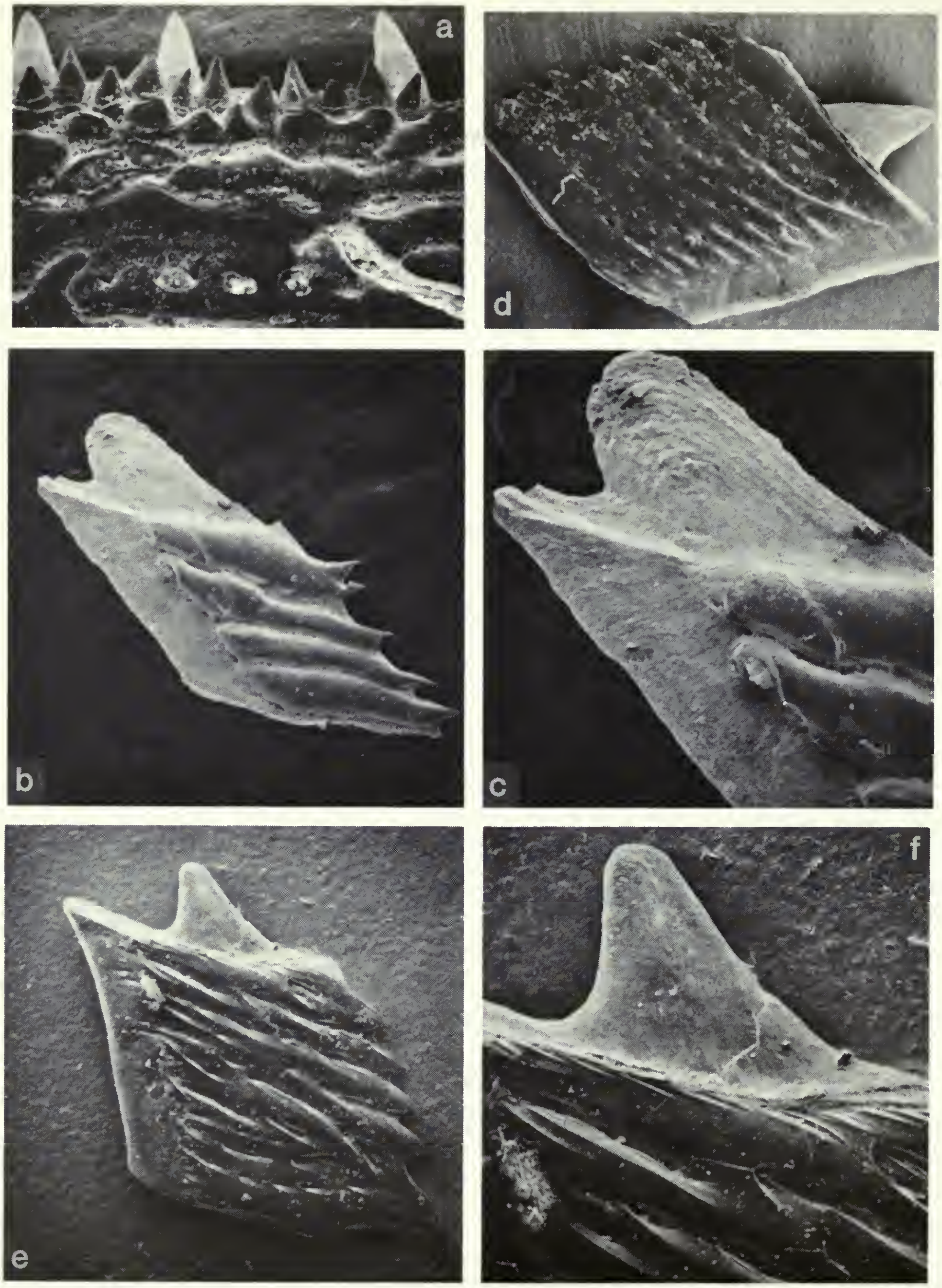

Plate 2 *Mimia toombsi* Gardiner & Bartram. (a) anterior end of dentary, from BMNH P.53252, × 30. (b) posterior abdominal scale, from Western Australian Museum no. 70.4.245 (holotype), ×35. (c) enlarged view of scale peg, same specimen, × 70. Scanning electron micrographs.

Moythomasia durgaringa Gardiner & Bartram. (d) anterior flank scale, from Western Australian Museum no. 70.4.244, × 25. (e) anterior scale, from BMNH P.53221, × 18. (f) enlarged view of scale peg, same specimen, × 42. Scanning electron micrographs.

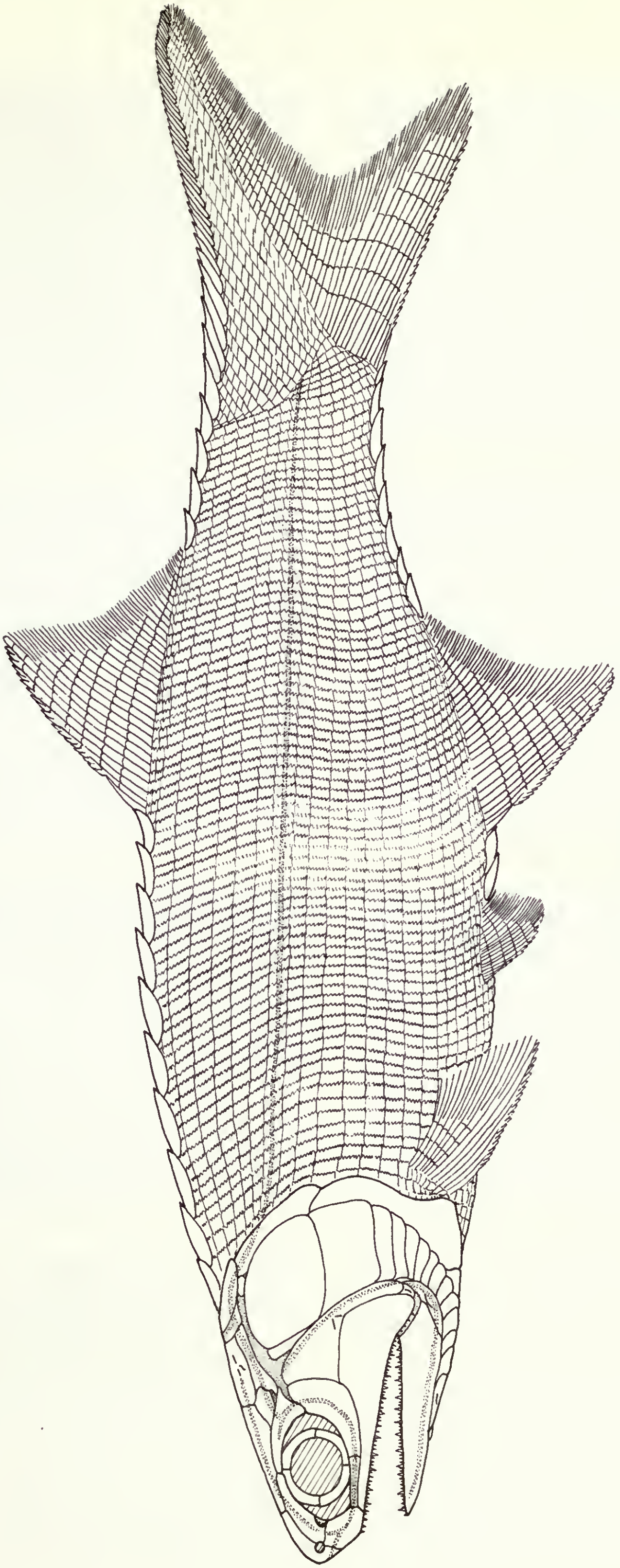

Fig. 145 *Mimia toombsi* Gardiner & Bartram. Restoration in lateral view.

margin. The scales of *Moythomasia* (Jessen 1968), like those of *Polypterus*, have a very thin layer of ganoine, with superposed generations of buried ganoine mostly confined to the scale margins. Thus the primitive actinopterygian scale seems to have grown by the addition of ganoine to the circumference rather than in the concentric 'onion-skin' fashion so typical of *Lepisosteus*. All primitive actinopterygian scales possess a superficial layer of ganoine which is said to be characteristic of actinopterygians (Schultze 1977, Patterson 1982). Slender peg-and-socket articulations between scales are also characteristic of actinopterygians but their absence from the scales of *Cheirolepis* is considered primitive. Nevertheless, the scales of *Cheirolepis* have a diagonal long axis and an anterodorsal process. A similar diagonal long axis and anterodorsal process characterize the scales of most actinopterygians (palaeoniscids, *Polypterus, Lepisosteus*) and is therefore considered synapomorphous for the group (Patterson 1982).

The scales of sarcopterygians never grow in the concentric 'onion-skin' fashion seen in actinopterygians. Instead they are of the cosmoid type with a superficial layer of enamel (Schultze 1977). Cosmine (dentine + enamel) is a hard tissue which encloses a complex pore-canal system. No living fish has either cosmine or a pore-canal system in the scales but the presence of both is regarded as a synapomorphy of rhipidistians and dipnoans (Rosen *et al.* 1981). The mesh canals linking the flask-shaped pore-canals have a horizontal partition in some osteolepiforms (Gross 1956) and this appears to be a specialization. Cosmine is missing from the scales of actinistians and tetrapods, but the scales of *Latimeria* do possess superficial tubercles which fuse to the scale surface. Separate tubercles occur above the scales in *Polypterus, Lepisosteus* and silurids. The scales of the dipnoan *Uranolophus* (Denison 1968, 1969) are characterized by Westoll-lines and superposed generations of tubercles.

The scales of euselachian chondrichthyans are typically placoid. Composite scales, however, occur in a Permian edestid holocephalian and the dorsal scales of '*Orodus*' (Ørvig 1966) grew in 'onion-skin' fashion by the presumed concentric addition of dentine to the crown and fibrous bone to the base.

Placoderms are usually devoid of scales, but where they occur they are often small and rhomboidal (Miles & Westoll 1968).

The scales of acanthodians are small, closely fitting and made of concentric layers of bone and dentinal tissue. They had an 'onion-skin' mode of growth, similar to that in actinopterygians (Gross 1966, 1973). In the *Nostolepis* type the crown is mesodentine (Ørvig 1967*b*) and in the *Acanthodes* type it is dentine. In *Poracanthodes* there is a pore-canal system, but its architecture is quite unlike that of rhipidistians and dipnoans.

Within the gnathostomes this 'onion-skin' mode of scale growth is considered primitive.

2. *Basal fulcra*

The large paired or unpaired scale-like structures, preceding the bases of the median fins in primitive actinopterygians (Patterson 1982), are termed basal fulcra; they appear to be modified ridge scales. They are particularly well developed on the dorsal border of the tail in those primitive actinopterygians without elongate upper caudal fin-rays (most palaeoniscids, *Mimia* and chondrosteans). They are also present in *Dapedium, Lepisosteus, Eurycormus, Caturus, Ionoscopus* (Patterson 1973), parasemionotids and primitive teleosts. Basal fulcra are absent in *Polypterus* but this is presumed to be secondary and related to the acquisition of a diphycercal tail.

Basal fulcra may be found in front of all the unpaired fins, including both lobes of the caudal (*Cheirolepis, Elonichthys, Cornuboniscus, Mesopoma*, sturgeons, *Dapedium* etc.), or they may be missing from the anal (*Moythomasia, Phanerosteon*), or from both anal and dorsal

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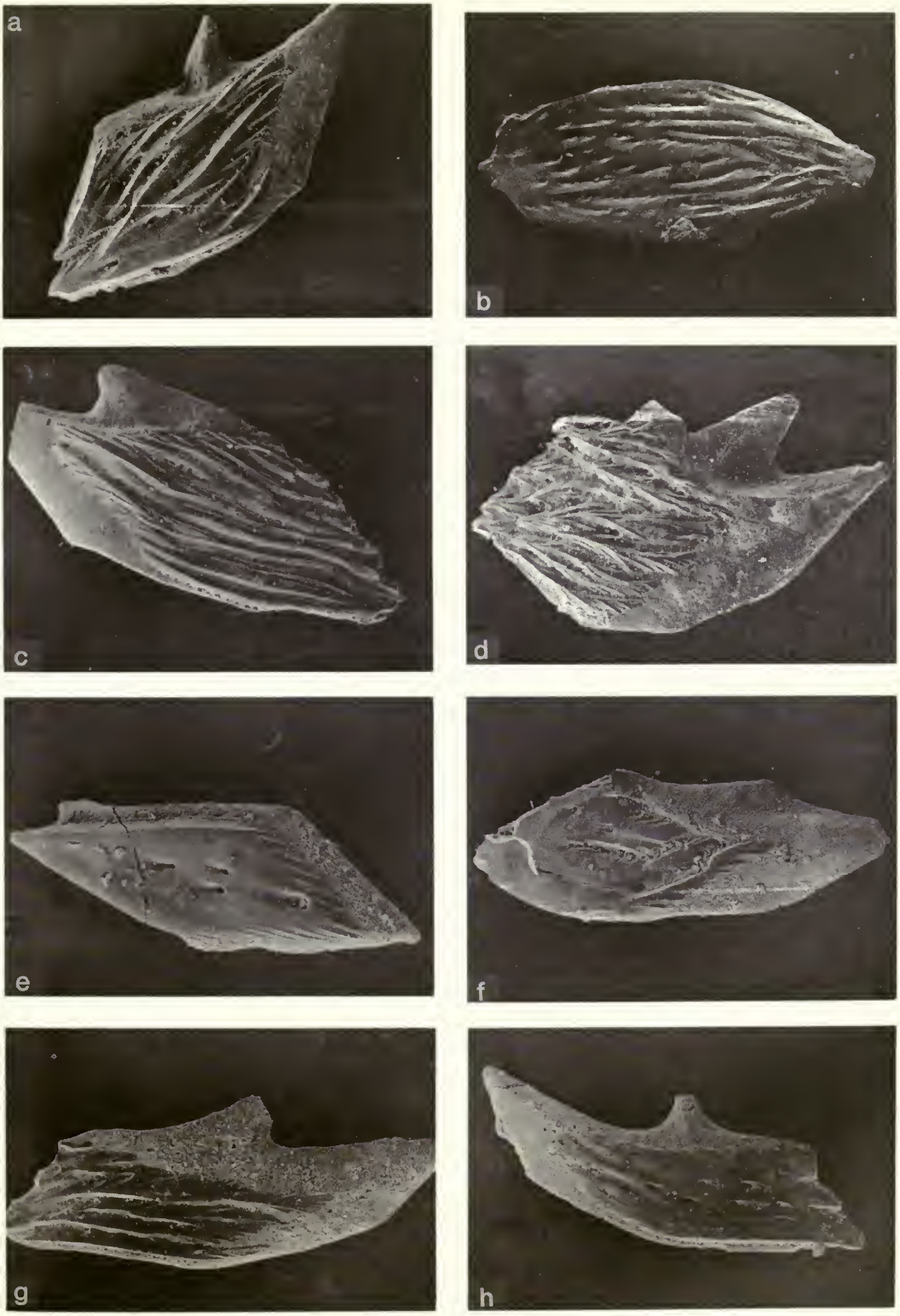
Plate 3 *Moythomasia durgaringa* Gardiner & Bartram, body scales. (a) mid-flank, ×27. (b) basal fulcral, ×16. (c) posterior flank, ×27. (d) anterior flank, ×27. (e) from base of tail, ×27. (f) from tail, ×27. (g) from base of anal fin, ×34. (h) from base of pelvic fin, ×27. Scanning electron micrographs, (a), (b), (d), (e), (f), (g) and (h) from BMNH P.56502, (c) from BMNH P.56475.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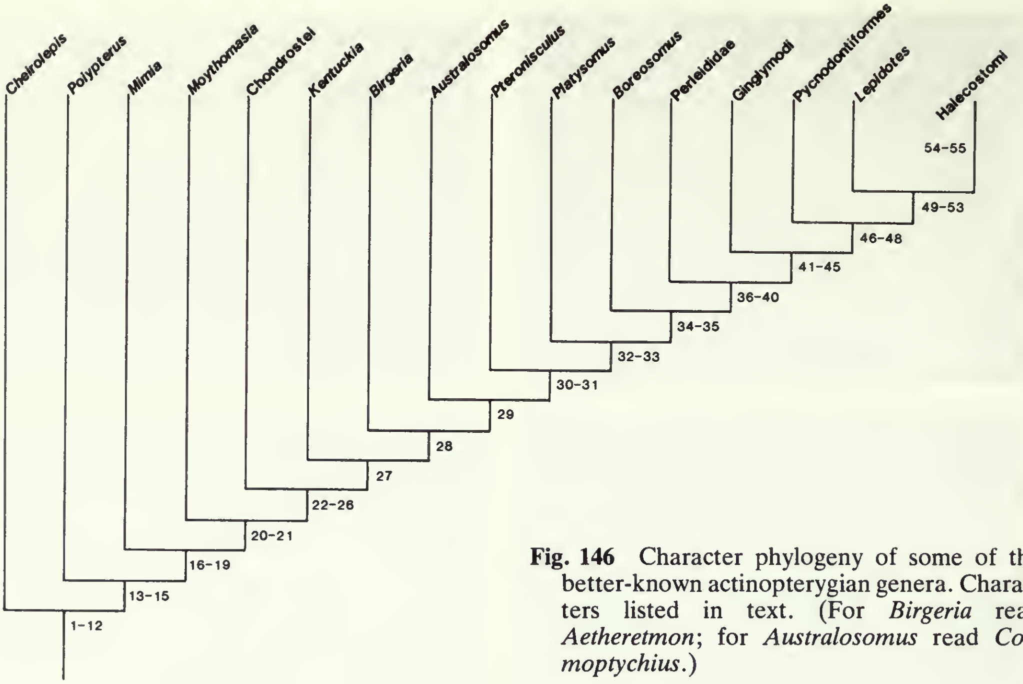
Cheirolepis
Polypterus
Mimia
Moythomasia
Chondrostei
Kentuckia
Birgeria
Australosomus
Pteronisculus
Platysomus
Boreosomus
Perleididae
Ginglymodi
Pycnodontiformes
Lepidotes
Halecostomi
54-55
49-53
46-48
41-45
36-40
34-35
32-33
30-31
29
28
27
22-26
20-21
16-19
13-15
1-12

Fig. 146 Character phylogeny of some of the better-known actinopterygian genera. Characters listed in text. (For *Birgeria* read *Aetheretmon*; for *Australosomus* read *Cosmoptychius*.)

(*Carboveles, Platysomus, Pygopterus, Polyodon, Lepisosteus*, generalized teleosts etc.), or from anal, dorsal and lower caudal (*Cryphiolepis*, haplolepids), or missing altogether (*Polypterus*, many teleosts). The basal fulcra are unpaired except above the tail in *Cheirolepis* where the first two scales are unpaired and the remaining 40–50 paired.

A single unpaired structure occurs in front of the median fins of *Osteolepis* and at least the dorsal fins of *Uranolophus*. However, only actinopterygians possess the long row of basal fulcra on the dorsal margin of the tail and these must be considered synapomorphous for actinopterygians (Patterson 1982).

3. *Fringing fulcra*
These are paired, leaf-like structures attached to the leading fin-rays which in fossils are difficult to distinguish from the dichotomously branched ends of the lepidotrichia. Fringing fulcra are unique to actinopterans but their distribution is very spasmodic. They are found in *Mimia, Moythomasia, Pteronisculus, Perleidus, Ptycholepis,* redfieldiids, *Lepisosteus*, many fossil neopterygians and primitive teleosts (upper margin of tail in *Megalops* and *Tarpon*), but are absent in *Tegeolepis, Cheirolepis, Styracopterus, Amia, Polypterus*, chondrosteans, pycnodonts and most living teleosts.

In *Elonichthys* the fringing fulcra are delicate with up to two pairs per lepidotrichial segment in *E. robisoni*. In *Lepisosteus* and *Meidiichthys* (BMNH P.1607) the basal fulcra grade into fringing fulcra and in many fossil actinopterans (parasemionotids, *Caturus, Semionotus, Dapedium, Ophiopsis*) the fringing fulcra are particularly stout and form a sturdy ‘cutwater’.

Phylogenetic results

Interrelationships of actinopterygians

Although most recent authors have regarded the Cladistia as actinopterygians (Goodrich 1930, Daget 1950, Gardiner 1973, Rosen *et al.* 1981, Forey & Gardiner 1981), some authorities have considered them a separate group of osteichthyans (Jarvik 1942, 1980, Nelson 1969*b*). Patterson (1982), in a critical examination of the evidence, concluded that they are the sister-group of

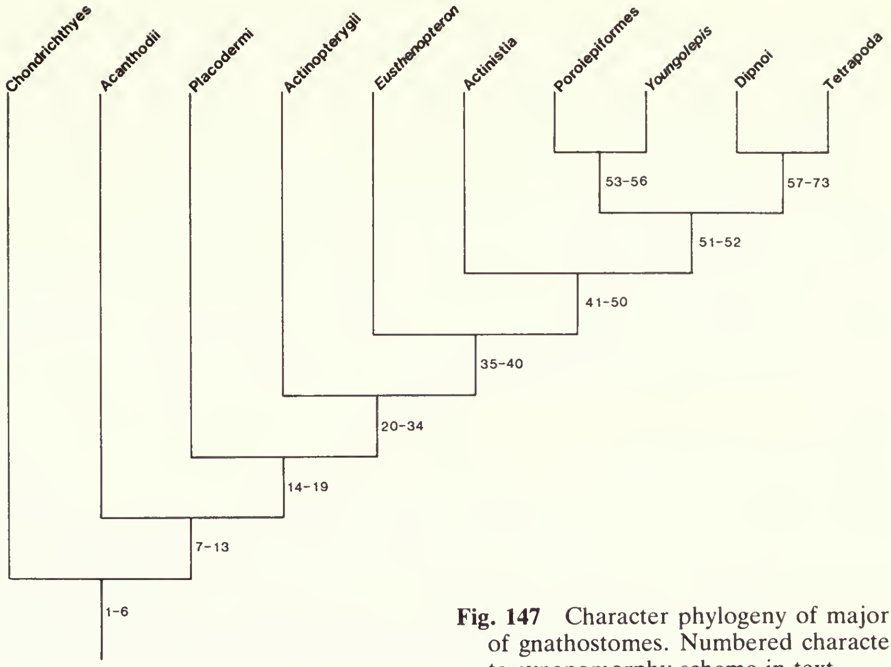

Fig. 147 Character phylogeny of major groups of gnathostomes. Numbered characters refer to synapomorphy scheme in text.

Actinopteri and this view is supported by the numerous synapomorphies listed by him. These include teeth with an apical cap of acrodin, the reduction of the jugal canal to a horizontal pit-line and the absence of a squamosal, presence of a valvula, otoliths formed of vaterite, gill-arch and jaw musculature, a protractor hyomandibularis muscle and pectoral propterygium.

Cladistia also share with Actinopteri buried layers of ganoine on the surface of dermal bones and ganoid scales with an anterodorsal process and peg-and-socket articulations. These characters are missing from living Chondrostei; however, there is an anterodorsal process on the scales of *Chondrosteus* (BMNH P.41615) and I have also observed small pustules of ganoine on some of the head bones of *Chondrosteus*. Since *Chondrosteus* is the sister-group of the Acipenseridae (Patterson 1982: 253) the absence of these characters in Chondrostei must be rated as secondary.

Other features common to cladistians and generalized actinopterygians, but absent in Chondrostei, include a dentary with an enclosed sensory canal, a dermohyal, presupracleithrum, a shield-like rostral with an enclosed ethmoid commissure, a dilatator operculi muscle and a levator arcus palatini muscle inserting on the dorsolateral surface of the palate.

Finally, cladistians share with Actinopteri, including chondrosteans, a parasphenoid with an ascending process and a posterior stem. I have argued elsewhere (Gardiner 1973: 116, and above) that the parasphenoid has grown back independently on several occasions, and conclude that the posterior stem in cladistians in non-homologous with that of chondrosteans which in turn is non-homologous with that of other Actinopteri. I also regard the ascending processes as non-homologous in cladistians and actinopterans. In actinopterans the ascending process is developed in the spiracular groove, whereas that in cladistians is large and complicated with medial, lateral and ventral components and has a different phylogenetic history (Patterson 1982).

Within the Actinopteri the Chondrostei and Neopterygii are generally regarded as sister-groups (Nelson 1969*b*; Patterson 1973, 1982). Shared synapomorphies include a spiracular canal which opens into the fossa bridgei, an ascending process of the parasphenoid which reaches or enters the spiracular canal, a supramedullary hemopoietic organ (presumed to occupy the lateral cranial canal of fossil forms), three ossifications or cartilages in the hyoid bar, a swimbladder and nasal rosette, a perforated pectoral propterygium embraced by marginal rays, a middle region to the endoskeletal pectoral girdle, and a dermopterotic.

In summary, if only Recent fishes are considered the most economical distribution of character states places Cladistia as the sister-group of Chondrostei plus Neopterygii.

The Neopterygii may further be divided into Ginglymodi and Halecostomi (Patterson 1973). Neopterygian synapomorphies include:

symplectic developed as an outgrowth of the hymandibular cartilage;
quadratojugal which braces the quadrate;
premaxilla with an internal process lining the nasal pit;
reduction of body lobe of tail;
symmetrical caudal fin in which the outer principal rays of the upper lobe approximately equal those of the lower lobe in length;
dorsal and anal fin-rays equal in number to their endoskeletal supports;
antorbitals;
articular with a coronoid process;
dermal basipterygoid process;
hyomandibula with opercular process;
palatoquadrate disconnected from dermal cheek bones posteriorly and dorsally;
preopercular with narrow dorsal limb no longer in contact with the maxilla.

Primitively in actinopterygians the palatoquadrate is assumed to have been tied to the maxilla anteriorly, the propercular dorsally and the quadratojugal posteriorly, thereby entirely enclosing the adductor mandibulae muscle in a tube of bone. Although the preopercular is missing in chondrosteans the adductor mandibulae muscle is still inserted on the outer surface of the palatoquadrate as in selachians. However, in neopterygians, where both dorsal and posterior contacts between the dermal cheek bones and the palatoquadrate have been lost, the adductor mandibulae is inserted on the neurocranium as well as the palatoquadrate. In cladistians, although contact is maintained between the palatoquadrate and preopercular posteriorly, the palatoquadrate turns inwards dorsally, not outwards as in acanthodians, selachians and chondrosteans, to lie in a nearly horizontal position with its edge fitting into a groove on the parasphenoid (a unique condition). The adductor mandibulae muscle is inserted on the preopercular, palatoquadrate, hyomandibula and neurocranium. I consider the loss of the dorsal connection between the palatoquadrate and preopercular and the concomitant insertion of the adductor muscle on the neurocranium to have occurred independently in cladistians and in neopterygians.

In halecostomes the anterior connection between the palatoquadrate and maxilla is also lost and the group is characterized by a mobile maxilla with a peg-like internal head. Other synapomorphies include:

enlarged posterior myodome occupying at least half the distance between the pituitary fossa and the vagus foramen;
pre-ethmoids;
large post-temporal fossa without an endoskeletal roof;
supramaxilla and interopercular;
epibranchials with uncinate processes;
intercalar with membranous outgrowths over the surface of the otic region;
loss of the quadratojugal as an independent element;
development of a post-temporal process.

A post-temporal process is also said to be present in *Polypterus* (Allis 1922: 206) and *Lepisosteus* (Jessen 1972: pl. 9, fig. 4), but these processes bear little resemblance to those in halecostomes and are therefore regarded as convergent.

Having outlined a phylogeny of Recent actinopterygians it is now possible to establish the approximate order of origin of specializations within the group.

The order Palaeonisciformes is generally considered to include the most primitive actinopterygians (Kasantseva-Seleznevak 1981) and *Mimia* and *Moythomasia* have both been assigned to that Order (Gardiner 1973). In the past most of the propositions of relationships of palaeoniscids have been couched in ancestor–descendent sequences (e.g. Gardiner 1963, 1967), but a cladistic examination (Patterson 1982) has revealed that the palaeoniscids constitute a paraphyletic group. It further showed that *Cheirolepis* is the sister-group of the Actinopterygii, *Mimia* is the sister-group of the Actinopteri + *Moythomasia*, but that the vast majority of the palaeoniscids are more closely related to the Neopterygii. It also revealed one major anomaly, the absence of a posterior myodome in *Lepisosteus*. A posterior myodome is present in all advanced palaeoniscids and in halecostomes (apart from a few teleosts where it is assumed to have been secondarily lost). However, from the congruence of other features, its absence in *Lepisosteus* is rated as secondary.

The advanced features are now listed in their approximate order of origin in a synapomorphy scheme which is summarized in Fig. 147 and in the classification.

A. *Cheirolepis* shares with other actinopterygians:
1. An anterodorsal angle or process to the scale
2. Ganoine
3. Dentary with enclosed mandibular sensory canal
4. Jugal canal not joined to infraorbital canal (except in *Polyodon*); instead it is reduced to a horizontal pit-line
5. Squamosal absent
6. Palatoquadrate joined to preopercular dorsally, and to quadratojugal posteriorly
7. Dermohyal covering head of hyomandibula only
8. Presupracleithrum
9. Pectoral propterygium
10. Otoliths formed of vaterite
11. A shield-like rostral with enclosed sensory canal commissure (except Chondrostei)
12. Basal fulcra on upper border of tail.

B. *Polypterus* has the foregoing characters (except 12) and shares with actinopterans:
13. Acrodin caps on all teeth
14. Peg-and-socket articulations between scales
15. Postcleithrum.

C. *Mimia* has all the foregoing characters (except 13: some teeth without caps) and shares the following derived features with Recent actinopterans:
16. Perforated propterygium
17. Bases of marginal rays embrace propterygium
18. A middle region to pectoral girdle
19. Lateral cranial canal.

D. *Moythomasia* has all the foregoing characters and shares the following derived characters with Recent actinopterans:
20. An ascending process on the parasphenoid which lies in the spiracular groove
21. Supra-angular.

E. Chondrostei have the foregoing characters apart from 3, 4, 6, 7, 8, 11, 14, 15 and 19, and share with neopterygians:
22. A spiracular canal
23. An ascending process which reaches or enters spiracular canal
24. A fossa bridgei
25. A dermopterotic
26. Three ossifications or cartilages in the hyoid bar.

It is worth noting that Patterson (1982) has recorded acrodin caps on the teeth of large

Polyodon, a supra-angular in *Chondrosteus* and I have observed ganoine on the dermal bones of *Chondrosteus* and scales with an anterodorsal angle.

F. *Kentuckia* has the characters of A–E (except perhaps 24, but characters 8, 9, 10, 12, 15, 16, 17, 18, 21, 26 not known) and shares the following derived character with primitive neopterygians:

27. Myodome.

G. *Aetheretmon* has the foregoing characters apart from 8 and 15 (19 not known) and shares the following derived character with neopterygians:

28. Suborbitals.

H. *Cosmoptychius* has the foregoing characters apart from 8 and shares the following derived character with neopterygians:

29. Unpaired myodome.

I. *Pteronisculus* has the foregoing characters and shares the following derived characters with neopterygians:

30. Dermal basipterygoid process
31. 'Prismatic' ganoine.

The term 'prismatic ganoin' has been used by Ørvig (1967*a*, 1978) to describe the appearance, when viewed by polarized light, of the superposed generations of ganoine on the scales and dermal bones of many palaeoniscids and neopterygians. I have seen this type of ganoine on the scales of many palaeoniscids including *Elonichthys, Rhadinichthys, Gonatodus, Palaeoniscus, Acrolepis, Gyrolepis, Pygopterus, Centrolepis, Eurynotus* and *Pteronisculus*. It was not seen in *Cheirolepis, Polypterus, Mimia, Moythomasia, Stegotrachelus* or *Australosomus*.

Many Carboniferous palaeoniscids appear to be either interchangeable with or to fit somewhere near *Pteronisculus* in this cladogram; these include *Elonichthys, Rhadinichthys, Gonatodus* and *Kansasiella*. Unfortunately, the characters for which information is available do not provide sufficient evidence for establishing hypotheses of relationships.

J. *Platysomus* has the foregoing characters apart from 6, 7, 8, 11 and 28 (9, 10, 16, 17, 18, 19, 22, 24, 26, 29 not known), and shares the following derived characters with neopterygians:

32. Palatoquadrate detached from preopercular and maxilla dorsally and from the preopercular posteriorly
33. Preoperculum and hyomandibula almost vertical.

K. *Boreosomus* has all the foregoing characters with the exception of 6, 7, 8 and 15. It shares the following derived features with neopterygians:

34. Hyomandibula with an opercular process
35. Fringing fulcra on upper border of tail.

The tail of *Boreosomus* is abbreviate heteroceral, with the body axis not quite reaching the end of the dorsal lobe. On the upper border basal fulcra appear to grade into fringing fulcra, much as in *Lepisosteus*. An opercular process also occurs in *Polypterus* but this is rated as convergent.

Boreosomus marks the end of the grade group (stem-group) Palaeonisciformes, but between it and the neopterygians are several more advanced groups formerly designated 'subholosteans'. These include the Perleididae. Other 'subholosteans' such as the Redfieldiidae are either interchangeable with or fit somewhere near *Boreosomus* in the phylogeny.

L. Perleididae have all the foregoing characters apart from 6, 7 and 8 (29 not known) and share the following derived characters with neopterygians:

36. Elongate upper caudal fin-rays
37. Dorsal and anal fin-rays equal in number to their supports
38. Antorbitals and premaxillae

39. Premaxilla with an internal (nasal) process which lines the nasal pit
40. A dilatator fossa.

The dorsal and anal fin-rays also equal their supports in haplolepids, *Bobasatrania, Luganoia* and *Platysiagum*.

M. Ginglymodi have all the foregoing characters except 6, 7, 27 and 29 and uniquely share with halecostomes:

41. A sympletic developed as an outgrowth of the hyomandibular cartilage and a quadratojugal which braces or supports the quadrate
42. Body lobe of tail reduced, symmetrical caudal fin in which outer principal rays of upper lobe approximately equal in length those of lower
43. Maxilla and preopercular lose contact with posterior margin of palatoquadrate
44. Articular with coronoid process
45. Preopercular with a narrow dorsal limb.

A coronoid process is developed in *Polypterus*, where it is composed solely of the prearticular. This is considered convergent with that of neopterygians which always incorporates lateral investing bones. The coronoid process of *Luganoia* is considered synapomorphous with that of neopterygians.

N. Pycnodontiformes have all the foregoing characters apart from 6, 7, 8, 11, 12, 15, 21, 28 and 35 (18, 19, 22, 24, 30, 31, 40 and 41 not known) and uniquely share with halecostomes:

46. A mobile maxilla with peg-like internal head
47. A large posterior myodome
48. Large post-temporal fossa.

In *Macromesodon* (Nursall 1966) the preopercular canal appears to have joined the infraorbital, much as in paddlefishes; this is assumed to be secondary. Although the jaw articulation is not known with certainty, there is a rod-like bone buttressing the quadrate in *Microdon* which has the appearance of a quadratojugal.

O. *Lepidotes* has the foregoing characters apart from 6, 7, 9 and 11 (16 not known) and uniquely shares with halecostomes:

49. A supramaxilla
50. An interopercular
51. Epibranchials with uncinate processes
52. A post-temporal with an internal process of halecostome type
53. Post-temporal fossa confluent with fossa bridgei.

Epibranchials with uncinate processes also occur in *Australosomus*.

P. Halecostomi have all of the foregoing characters except 6, 7 and 11, and in addition possess:

54. An intercalar with membranous outgrowths over the surface of the otic region
55. A quadratojugal which no longer remains as an independent element.

Classification

The broad phylogenetic results based on the synapomorphies cited in the text are summarized in the following outline classification, which follows the conventions of Patterson & Rosen (1977). '†' indicates an extinct group.

SUPERCLASS Gnathostomata
  CLASS Chondrichthyes
    SUBCLASS Selachii
    SUBCLASS Holocephali
  Plesion †Acanthodii
  Plesion †Placodermi
  CLASS Osteichthyes

SUBCLASS Actinopterygii
  INFRACLASS Cladistia
  INFRACLASS Actinopteri
    SUPERDIVISION Chondrostei
    SUPERDIVISION Neopterygii
      DIVISION Ginglymodi
      DIVISION Halecostomi
        SUBDIVISION Halecomorphi
        SUBDIVISION Teleostei
SUBCLASS Sarcopterygii
  Plesion †*Eusthenopteron*
  INFRACLASS Actinistia
  Plesion †Akinetia
        ORDER †Porolepiformes
        ORDER †Youngolepiformes
  INFRACLASS Choanata
    SUPERDIVISION Dipnoi
    SUPERDIVISION Tetrapoda

The more particular results concerning the interrelationships of actinopterygians are embodied in the classification below.

SUBCLASS Actinopterygii
  Plesion †*Cheirolepis*
  INFRACLASS Cladistia
  INFRACLASS Actinopteri
    Plesion †*Mimia*
    Plesion †*Moythomasia*
    SUPERDIVISION Chondrostei
    SUPERDIVISION Neopterygii
      Plesion †*Kentuckia*
      Plesion †*Aetheretmon*
      Plesion †*Cosmoptychius*
      Plesion †*Pteronisculus*
      Plesion †*Platysomus*
      Plesion †*Boreosomus*
      Plesion †Perleididae
      DIVISION Ginglymodi
      Plesion †Pycnodontiformes
      Plesion †*Lepidotes*
      DIVISION Halecostomi

Relationships of actinopterygians

A character phylogeny of Recent and fossil gnathostomes has been presented by Rosen *et al.* (1981), in which they have suggested that the acanthodians are the most plesiomorphous gnathostomes, lungfishes are the sister-group of tetrapods and that rhipidistians are paraphyletic and form a stem-group series between actinopterygians and lungfishes. The phylogeny given below is essentially that of Rosen *et al.* except that the chondrichthyans are considered the most plesiomorphic gnathostomes and the placoderms the sister-group of osteichthyans. In addition the Porolepiformes + *Youngolepis* are considered the sister-group of the dipnoans and tetrapods (see Fig. 147).

A. Chondrichthyans share with other gnathostomes:
  1. A lower jaw supported by a palatoquadrate and hyomandibula. Hyomandibula which contacts neurocranium

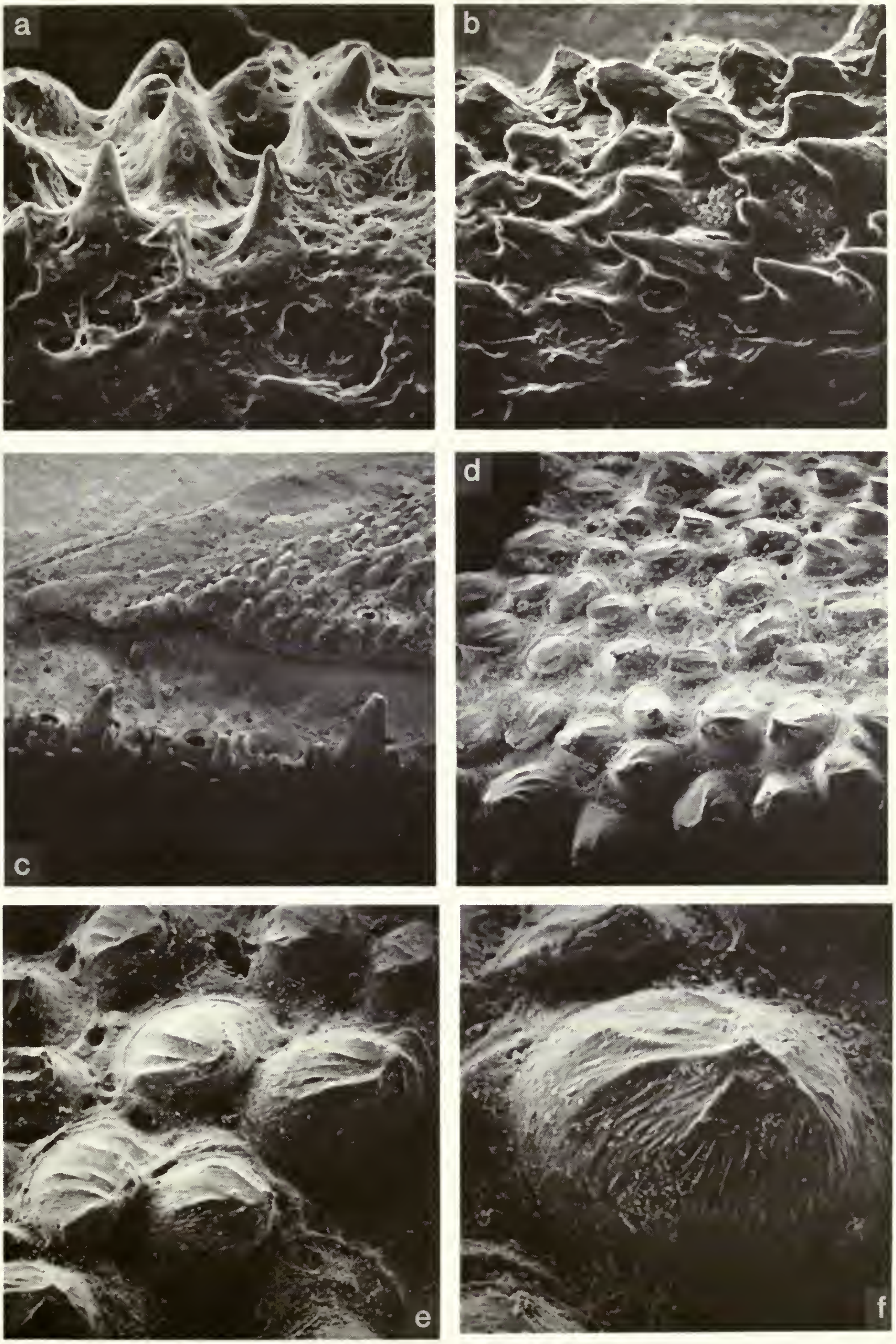

Plate 4 *Mimia toombsi* Gardiner & Bartram. (a), (b) coronoid teeth, ×150. (c) anterior end of palatine with accompanying maxillary tooth row, ×30. (d–f) palatine teeth, (d) ×100, (e) ×200, (f) ×500. Scanning electron micrographs, all from BMNH P.53252

2. A hyoid bar connecting the branchial apparatus with the hyomandibula
3. Anterior branchial arches consisting of hypobranchial which articulates with a basibranchial, ceratobranchial, epibranchial and pharyngobranchial elements
4. A cephalic lateral-line system that includes the following canal sections: supraorbital, infraorbital, supratemporal, mandibulo-preopercular, and jugal that joins the infraorbital and preopercular
5. Paired pectoral and pelvic appendages with internal supporting girdles and radials
6. Three semicircular canals.

B. Acanthodians also have the following derived features which they share with placoderms and osteichthyans:

7. Shoulder-girdle with ventral dermal plates and three perichondral ossifications
8. Operculogular series of dermal plates
9. Three ossfications in palatoquadrate
10. Two ossifications in Meckelian cartilage
11. Two ossifications in basibranchial cartilage
12. Dentigerous dermal plates on dorsal surface of Meckelian cartilage
13. Splenial bone.

The hypothesis that acanthodians and osteichthyans are sister-groups (Miles 1964, 1971*a*, 1973*a*) is supported by the presence of branchiostegal rays (8 above) and ventral dermal plates on the shoulder girdles (7 above), while the suggestion that they are the sister-group of chondrichthyans (Nelson 1968) is sustained by the posterior position of the gill skeleton and the posterior orientation of the pharyngobranchials. The double mandibular joint of *Acanthodes* is also said to be strikingly similar to that of amphistylic sharks (Miles 1973*a*: 71). The posterior position of the gill skeleton is a character shared only by selachians and acanthodians whereas the operculogular series and ventral plates of the shoulder girdle are found in acanthodians, placoderms and osteichthyans. The double jaw joint is seen in selachians, acanthodians and actinopterygians. However, since acanthodians uniquely share with placoderms and osteichthyans three ossifications in the palatoquadrate cartilage and two in the Meckelian cartilage, and have only a few ossification centres in the neurocranium, it seems more economical to interpret them as the sister-group of the osteichthyans + placoderms.

C. Placoderms have the foregoing characters apart from 13 (3, 11 not known) and share with osteichthyans:

14. Neurocranium protected by a series of large, interlocking dermal plates, some of which possess descending laminae of membrane bone
15. True dermal shoulder girdle with lateral plates to which scapulocoracoid is attached (viz. clavicle + cleithrum)
16. Supracoracoid foramen
17. Autopalatine articulates with postnasal wall
18. Dermal bone associated with the head of the hyomandibula (and completely covers the hyomandibula)
19. Parasphenoid with teeth, spiracular groove and foramen for buccohypophysial canal.

Evidence for the association of placoderms with osteichthyans has been presented by Forey (1980), who also cited the shared presence of endochondral bone. In my opinion (see p. 185) placoderms possess calcified cartilage, never endochondral bone. The competing hypothesis that placoderms and chondrichthyans are sister-groups (Stensiö 1963*a*, Miles & Young 1977) rests on two characters, the pelvic clasper and eye stalk.

Miles & Young (1977) have argued that pelvic and prepelvic claspers are most parsimoniously explained as a unique specialization of chondrichthyans plus placoderms. But only the ptyctodonts and holocephalans have both these structures. All other placoderms are devoid of claspers and selachians possess only pelvic claspers. Moreover the pelvic claspers in chondrichthyans consist of a varied number of articulated, cartilaginous segments supported by the distal end of the metapterygium, whereas that of ptyctodonts does not appear to have an endoskeleton, projects ventrally from the root of the fin, and is covered by a laterally-toothed dermal plate. Distally the pelvic claspers are covered with dermal denticles in holocephalans, but the apex is usually naked in selachians except in the squaloids etc., where it is provided with one or more movable spines. The prepelvic claspers in ptyctodonts, like the pelvics, are supported by dermal bone only. They consist of a pair of flat plates which in *Ctenurella* bear spines. The corresponding structure in holocephalans is represented by a cartilaginous plate (grooved in *Callorhynchus*) covered with dermal denticles. Because of their different construction the pelvic and prepelvic claspers are accordingly rated as non-homologous in chondrichthyans and ptyctodonts. Eye stalks, or their scars, have been recorded in three genera of rhenanids, *Radotina* (Gross 1958: fig. 5A; Stensiö 1969: fig. 51), *Romundina* (Ørvig 1975: pl. 2, figs 1, 2) and *Brindabellaspis* (Young 1980: pl. 1, fig. 5; pl. 2, fig. 6), in arthrodires (*Buchanosteus* Young 1979) and in ptyctodonts, and in many selachians (*Oxynotus, Scyllium*, various myliobatids; Holmgren 1941). There are never any scars in xenacanths or hybodonts. The eye stalk chondrifies independently in selachians (Holmgren 1940: 109) and often leaves no trace of a scar in the wall of the orbit (e.g. *Chlamydoselachus*). The non-congruence with all other characters suggests that the presence of eye stalks is either a primitive gnathostome attribute or a chance similarity.

Finally Schaeffer (1975) considered placoderms to be the most primitive gnathostomes, based on the structure of the palatoquadrate. He suggested that their 'omega-shaped' palatoquadrate, in direct contact with the dermal cheek bones (viz. without a lateral cavity for the insertion of the adductor mandibulae muscles), was the primitive condition. Forey (1980), in contrast, considered it a synapomorphy of placoderms. However, the palatoquadrate of ptyctodonts and gemuendinids can by no stretch of the imagination be considered either 'omega-shaped' or in direct contact with the dermal cheek bones. Furthermore the adductor mandibulae muscle must have been inserted on the lateral face of the palatoquadrate in both *Ctenurella* (Miles & Young 1977: figs 24–28) and *Jagorina* (Stensiö 1959: figs 61–64), much as in generalized gnathostomes. An 'omega-shaped' palatoquadrate is therefore rated as a specialization of later placoderms, setting them apart from the more primitive ptyctodonts and gemuendinids.

D. Actinopterygians have all the foregoing characters (but the dermohyal only covers the head of the hyomandibula) and share with other osteichthyans:

20. Endochondral bone
21. Marginal teeth associated with premaxilla, maxilla and dentary (dental arcades), some of which undergo successional replacement
22. Premaxilla canal-bearing
23. Lepidotrichia in the fins
24. Suprapharyngobranchials on the first two gill arches
25. Radials of fins never extending to the fin margin (except in tetrapods)
26. Interhyal
27. Hypohyal
28. Gular plates
29. Subopercular
30. Basibranchial with consolidated toothplates
31. Anteriorly-directed pharyngobranchials
32. Gill arches 1 and 2 articulating on the same basibranchial
33. Separate branchial levator muscles, interarcual muscles and transversi ventrali muscles
34. Lung or swimbladder.

Rosen *et al.* (1981) listed a dermal sclerotic ring as a synapomorphy at this level. However, a sclerotic ring also occurs in placoderms (four plates), acanthodians (five plates) and cephalaspids (four plates); see p. 253.

E. *Eusthenopteron* has the foregoing characters apart from 18 (but 33, 34 not known) and shares the following derived features with actinistians, porolepiforms, dipnoans and tetrapods:

35. Exclusively metapterygial pectoral and pelvic fins, supported by a single basal

36. Teeth with enamel
37. Sclerotic ring of more than 12 segments
38. Enlarged otic or ascending process of palatoquadrate which articulates or fuses with neurocranium above the basitrabecular process
39. Submandibulars
40. Hyomandibular facet bilobed or double.

The palatoquadrate also articulates with the neurocranium in *Acanthodes*, but the articulation point is behind the postorbital process and is therefore rated as convergent, as is the fusion of the palatoquadrate in holocephalans. Rosen *et al.* (1981) also cite the presence of an anocleithrum as a synapomorphy at this level.

F. Actinistians have the characters of A, B, C, D and E apart from 3, 16, 18, 27 and 39, and share with Porolepiformes, dipnoans and tetrapods:

41. An unornamented anocleithrum
42. Clavicle large relative to cleithrum, and high pectoral appendage insertion
43. Pectoral and pelvic appendages with long muscular lobes and structurally similar endoskeletal supports
44. Preaxial side of pectoral fin endoskeleton rotated to postaxial position
45. A series of bones (the supraorbital–tectal series) lateral to the frontals and nasals which carry the supraorbital sensory canal
46. Presence of a rostral organ or labial cavity
47. A single, broad basibranchial
48. Last gill arch articulates with base of preceding arch
49. Reduction or loss of hypobranchials
50. An inferior vena cava and pulmonary vein.

G-1. Porolepiformes have the foregoing characters (24, 33, 34, 43, 44, 46, 50 not known) apart from 16, 18, 45 and 49, and share with dipnoans and tetrapods:

51. The immobilization of the intracranial joint
52. Cosmine pore-canal system in which the mesh canals are without a horizontal partition and the pore canals are enamel-lined.

That the intracranial joint was immobilized in porolepiforms is deduced from *Glyptolepis* (Jarvik 1972), in which the palate is fused to the postnasal wall anteriorly, into the 'fossa autopalatina' medially and to the basipterygoid process posteromedially, and where the articulation between the ascending process and the neurocranium is absent. This deduction is strenthened by the suggestion (below; see Jessen 1975: 213) that the Youngolepididae (*Youngolepis* and *Powichthys*) is the sister-group of the porolepiforms, since a suture often exists between the two shields of the skull roof in *Youngolepis* (Chang 1982) despite the fact that the underlying endocranium is ossified as a single piece. Moreover most of the specimens of *Youngolepis* that have been collected (Chang 1982: 7) are separate anterior cranial portions, much as in porolepids.

G-2. Youngolepididae (*Youngolepis* + *Powichthys*) also uniquely share with porolepiforms:

53. A 'fossa autopalatina' (Chang 1982: pl. 15A)
54. Foramen for the pituitary vein anterodorsal to the basipterygoid process (Chang 1982: 77)
55. Vomers widely separated by internasal pits and parasphenoid; internasal ridge
56. Much enlarged, downwardly pointing basipterygoid process.

Powichthys also shares with actinistians and dipnoans a series of bones lateral to the frontals which carry the supraorbital canal. Youngolepids may be distinguished from porolepids by the non-dendrodont form of their teeth.

A phylogeny of Recent gnathostomes rates the intracranial joint as a unique feature of *Latimeria*. Nevertheless there are several hypotheses about this structure, some of which have been generated to satisfy the assumption that rhipidistians rather than lungfishes are closer to tetrapods.

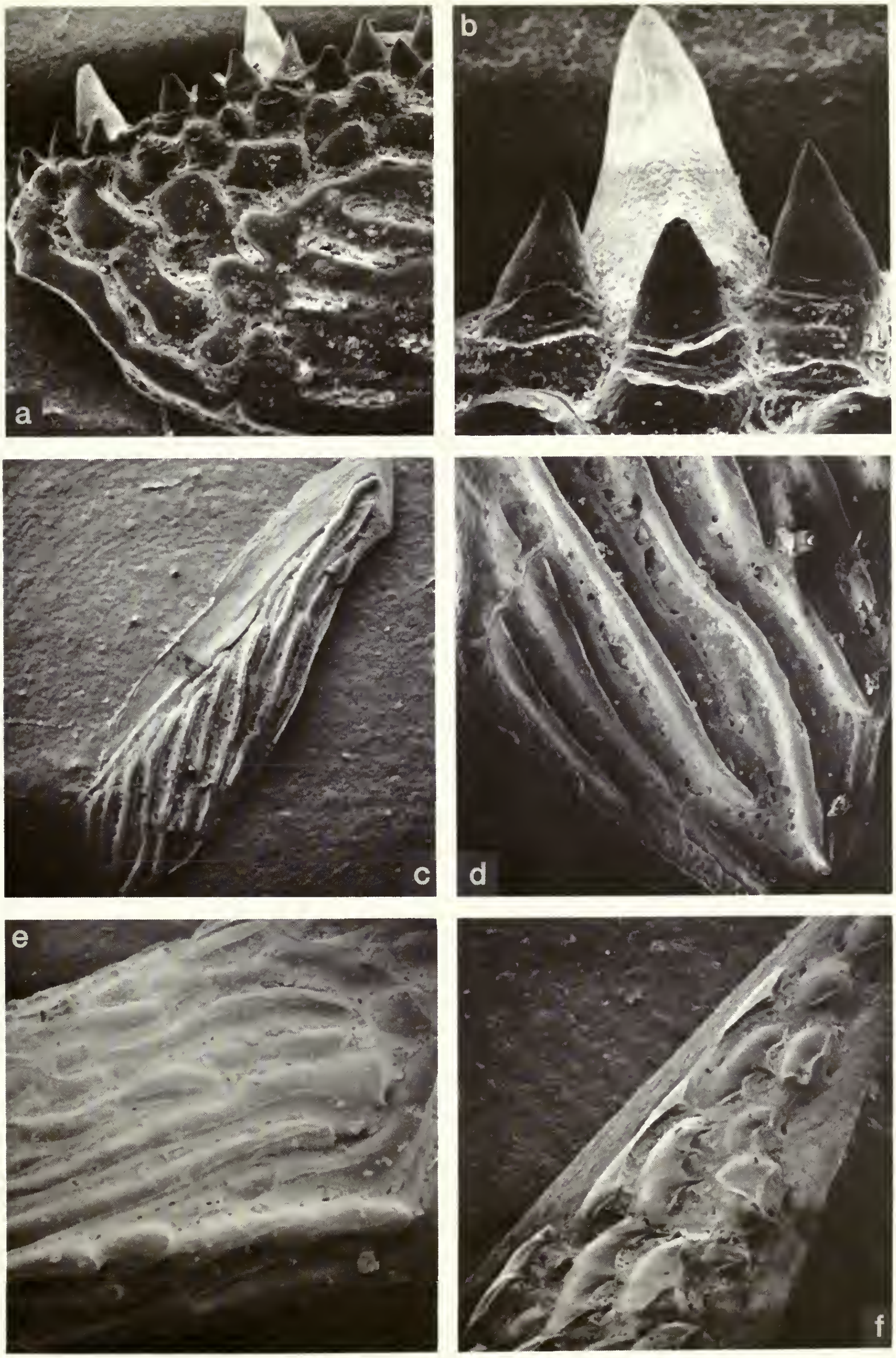

Plate 5 *Mimia toombsi* Gardiner & Bartram. (a) dentary tooth, ×30. (b) dentary tooth, ×150. (c) branchiostegal ray, ×20. (d) posterior tip of branchiostegal ray, ×60. (e) ornamentation of clavicle base, ×40. (f) dorsal spine of clavicle, ×100. Scanning electron micrographs, (a), (b) from BMNH P.53252, (c), (d) from BMNH P.56489, (e), (f) from BMNH P.56484.

The hypothesis that the intracranial joint is a primitive gnathostome character (Jarvik 1972) has been rejected because it leads to unacceptable phylogenetic conclusions (Miles 1977: 312; Forey 1980: 382). Another hypothesis, that it is a shared specialization of actinistians and choanates, separating this group from dipnoans (Miles 1977: 51), is also rejected, since no extant choanate possesses such a joint and its occurrence in fossil choanates is dubious (Rosen *et al.* 1981: 259; Gardiner 1983). The suggestion by Bjerring (1973) that the intracranial joint is not homologous in choanates and actinistians, which was arrived at by comparing the neurocrania of *Latimeria* and *Eusthenopteron* with the embryological condition in other gnathostomes, cannot be checked and is therefore regarded as speculation. The phylogeny outlined here interprets the intracranial joint as homologous in rhipidistians and actinistians, and therefore as a primitive feature of sarcopterygians. Further, it assumes that the joint has been lost once in porolepiforms (including youngolepidids) and choanates (dipnoans and tetrapods).

H. Dipnoans have all the foregoing characters except 2, 3, 18, 21, 22, 24, 26, 31 and 36, and those of G-2, and uniquely share with primitive tetrapods:

57. A choana
58. A labial cavity
59. Second metapterygial segment of paired appendages composed of paired, subequal elements that are functionally joined distally
60. Two primary joints in each paired appendage, between the endoskeletal girdle and the unpaired basal element, and between the basal element and the paired elements of the second segment. In the pectoral appendage, the preaxial member of paired elements with a ball-and-socket joint with the basal element and the postaxial member articulating on dorsal (postaxial) margin of basal element
61. Reduction in ratio of dermal fin-rays to supports in paired appendages
62. Muscles in paired fins segmented
63. Fusion of right and left pelvic girdles to form pubic and ischial processes. Presence of prepubic processes
64. Tetrapodous locomotion
65. Hyomandibula non-suspensory, reduced and associated with otic recess
66. Interhyal absent
67. Pharyngobranchials absent
68. Pterygoids joined in mid-line anteriorly, excluding parasphenoid from roof of mouth
69. Autopalatine absent
70. Elongation of snout region
71. Two pairs of dermal bones attached to the otico-occipital region of braincase posterior to parietals
72. Dentary with an oral pit-line
73. In soft anatomy, structure of lung, pulmonary circulation, two-chambered auricle, ventral aorta as a truncus, glottis and epiglottis, telolecithal jelly-coated bipolar egg, ciliation of the larva, pituitary structure including neurohypophysial hormone, lens proteins and bile salts, and gill-arch muscles.

Fusion of right and left pelvic girdles and prepubic processes also occur in many selachians, but this is considered convergent.

This phylogeny is summarized in the classification above (p. 399).

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